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# OBSERVATIONS ON THE INHERITANCE OF A MULTIFACTOR COLOR VARIATION IN WHITE-FOOTED MICE (*PEROMYSCUS*)

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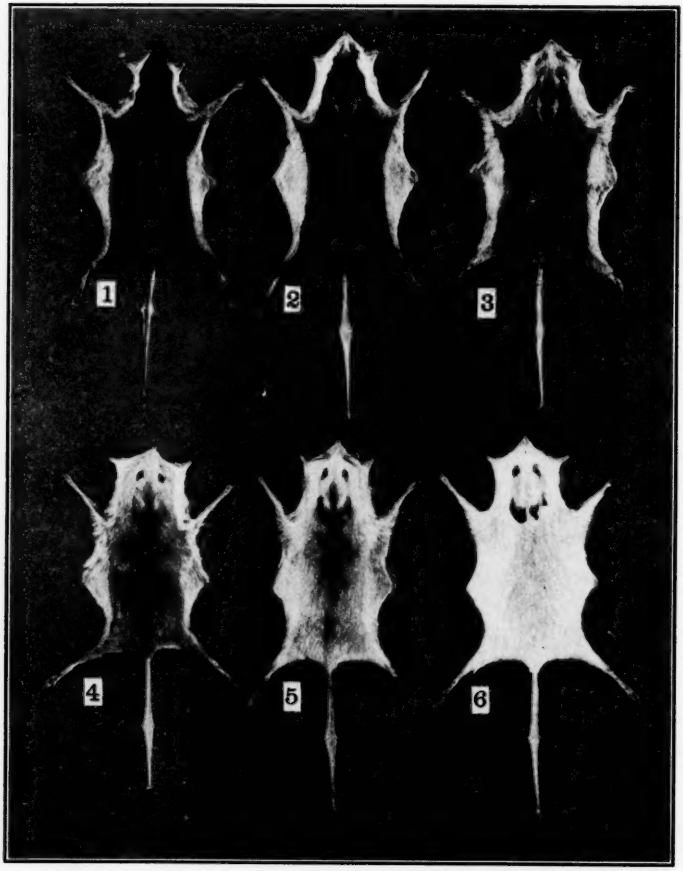
THE following account is concerned with the inheritance of a rather striking color variation of seemingly rare occurrence. The variation is one which offers interesting analogies with some other characters, both of mutant races and wild species. It has not previously been dealt with genetically or even described. Owing to these circumstances and to the further fact that I have definitely discontinued the breeding of this stock, it has seemed justifiable for me to publish the results of my rather extended observations, even though an adequate analysis into mendelian factors has been impracticable.

The color variation in question was first observed in my stock of *Peromyscus maniculatus gambelii* in 1916. It was briefly mentioned in a paper (1918) which was mainly concerned with other matters. "Grizzled" or "white-faced" individuals had at that time been noted in three successive generations, but the numbers were very limited, and little was learned regarding the inheritance of this character.

In 1920 two conspicuously grizzled individuals were discovered in a stock of *gambelii* which had been bred for other purposes by Dr. H. H. Collins and the writer. These two mice, both males, were, so far as known, unrelated to one another or to the previous examples of




1. Skin of "normal" (0) *Peromyscus maniculatus gambelii.*
2. Grizzled specimen, "moderate" (grade 3).
3. "Very pronounced" (grade 5).
4. "Extended A" (grade 6).
5. "Extended B" (grade 7).
6. "Extended C" (grade 8).

grizzled. Since, however, these animals were trapped in the same general neighborhood, it is not impossible that the genetic factors concerned were derived from common ancestors in the wild state.

It is with the descendants of these two later examples of grizzled that the present paper is concerned. They are designated in my records by the numbers $C_1$ ♂ 144 and $C_2$ ♂ 14. The former was one generation removed from the wild, the latter two generations. So far as the records indicate, the parents of both of these individuals were normal. The evidence on this point is not decisive, however, since the parent stock was not closely inspected for color aberrations, and the more feeble manifestations of the grizzled variation are readily overlooked. In subsequent experiments, affected individuals have invariably had at least one affected parent.

The name "grizzled" has been applied to an hereditary condition which results in the replacement of colored hairs by white hairs in certain parts of the pelage. In a large majority of my specimens this peculiarity has been restricted to the anterior end of the head and the dorsal stripe of the tail, the trunk not being visibly affected. All gradations exist, however, from a scarcely perceptible sprinkling of white hairs, near the tip of the snout, to a condition in which the head, trunk and tail are nearly devoid of pigmented hairs, and the appearance approaches that of an albino. But even these "ultra-grizzled" specimens are readily distinguished from the true albinos, for a quite appreciable number of dark hairs have always remained in the trunk region, while the eyes are black, and the ears and soles of the feet retain a normal amount of skin pigment.[1] In a number of cases the skin of the tail was likewise found to be rather heavily pigmented, a condition wholly lacking in most normal individuals, though previously observed more than once in non-grizzled stock (Sumner, 1918). These circumstances make it plain that grizzled mice, even of the most extreme type, have undergone no loss in the power of pigment production, except in so far as the hair is concerned. In this respect they appear to agree with the house-mice, described and figured by Hance (1927), which

[1] The *hairs* of the ears frequently become white, however.

underwent depigmentation of the pelage as a result of exposure to X-rays.

For the purposes of the present study the grizzled individuals have been divided into eight rather arbitrary grades, although, as already stated, a continuous series is actually encountered. The grading was done with reference only to the pelage of the head and trunk, the tail being left out of consideration. The grades adopted are: (1) trace, (2) slight, (3) moderate, (4) pronounced, (5) very pronounced, (6) extended A, (7) extended B, (8) extended C. In the first five of these grades the head only is affected, the area and intensity varying with the grade assigned. In the last three the pelage of the body is likewise whitened to an increasing extent. In the grade called "trace" the grizzling is confined to a small area at the anterior end of the snout, and even this may be scarcely perceptible. Indeed, many questionable cases are recorded which may well belong in the "normal" group. Grades 7 and 8 were collectively called "ultra-grizzled" during the breeding experiments, but it became evident that at least three grades could be distinguished having the body-color affected.

An interesting feature of the grizzled variation is its delayed appearance in the life of the individual. Commonly it was not noted until the age of six months or more, its time of manifestation probably corresponding with the assumption of the so-called "adult" (second post-juvenile) pelage. Indeed, the records for a few low-grade grizzled individuals list them as "normal" up to the age of twelve or fifteen months. These were, however, among the earliest records, and it is probable that slight traces of grizzling were at that time overlooked. On the other hand, some of the more extreme individuals displayed traces of grizzling on the snout as early as two or three months after birth. In general the more pronounced the case the earlier its appearance, though this was not always true. In some individuals the grizzling process continued relatively late in life. One of my more

pronounced cases did not reach the "extended" condition until the lapse of a year and a half and perhaps considerably longer.

For the foregoing reasons mice have been commonly excluded from my classified series unless they reached the age of twelve months. In a few exceptional cases (designated as doubtful in the table) records made at the age of nine months have been included.

It is probable that the assignment of grades seldom erred by more than one place in the series, despite the fact that no standard set of skins was available until toward the close of these studies, and that the observations extended over a period of several years. At best, however, any such mode of grading must be rather arbitrary.

Reference has already been made to the fact that the longitudinal dorsal stripe of the tail, which normally consists of black or brown hairs, was deficient or wanting in grizzled specimens.[2] It was further found that the grade of depigmentation of the tail-stripe corresponded roughly with the grade of grizzling of the pelage in general. In order to estimate the degree of this correlation, the tail stripes were graded, according to the extent of the modification, into three classes (0, 1 and 2), the first of these representing the normal condition. The mean grade of tail-stripe, for each of the grades of grizzling (1–8) together with that for normal ("0" grade) derivatives of grizzled parents, is given herewith:

| | | | |
|---|---|---|---|
| 0 | 0.22 | 5 | 2.00 |
| 1 | 0.82 | 6 | 1.71 |
| 2 | 1.32 | 7 | 2.00 |
| 3 | 1.17 | 8 | 2.00 |
| 4 | 1.50 | | |

That this correlation between the degrees of grizzling on different parts of the body is due merely to the generalized effects of the same factor or factors might be regarded as almost self-evident. This is quite questionable, however. For, on the one hand, there are a number

[2] This was likewise noted in the 1916–17 series.

of partially depigmented tails among the group with otherwise normal pelages, and on the other hand, there are seemingly normal tails, belonging to mice with grizzled pelages, even to one as high in the scale as grade 6. The data would seem to accord better with the assumption that the correspondence is due to the action of factors which are linked rather than to identical factors. In this connection it may be stated that occasional individuals have been encountered in non-grizzled stock, belonging to several different subspecies, which have manifested this same phenomenon of replacement of black by white hairs in the tail stripe. In one case, at least, it seems probable that the character was hereditary.

Breeding experiments with the grizzled stock were commenced in the fall of 1920, and were continued until the fall of 1925. In the spring of 1927 the studies were finally abandoned, part of the material being killed, and the remainder sent to Dr. Lee R. Dice, of the University of Michigan.[3] The grizzled variant, like the other color "mutations" already reported upon (Sumner, 1917, 1918; Sumner and Collins, 1922), was a by-product of experiments having quite other objects in view, so that no great amount of time or shelf-space was available for its investigation. Furthermore, an unusually large proportion of this particular stock proved to be sterile, and thus matings of critical importance were frequently without issue. Nevertheless, during the period here considered, about 175 individuals were reared to maturity and subjected to observation.

The various matings which were made, together with the resulting offspring, are indicated in Table 1.

Some of the salient features of the heredity of this character, as revealed by this table, are as follows:

(1) Every grizzled parent here considered bore (or sired) some grizzled offspring. This occurred even in those (thirteen) cases where grizzled individuals were

[3] These are now in charge of Dr. H. W. Feldman, who has kindly furnished me additional information regarding the derivatives of two matings.

TABLE 1*

RESULTS OF VARIOUS TYPES OF MATINGS

| Mother | Father | Offspring | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Normal (0) | Trace (1) | Slight (2) | Moderate (3) | Pronounced (4) | Very Pronounced (5) | Extended A (6) | Extended B (7) | Extended C (8) |
| ♀ 46 (normal, of grizzled parentage) | ♂ 57 (normal, of grizzled parentage) | 2 | | | | | | | | |
| ♀ 44 " " " " | ♂ 57 " " " " | 5 | | | | | | | | |
| ♀ 40 " " " " | ♂ 53 " " " " | 1 | | | | | | | | |
| | Total ..... | 8 | | | | | | | | |
| ♀ 6 (trace) | ♂ 2 (normal, of grizzled parentage) | 4 | 1 | | 3 | 1 | | | | |
| ♀ 9 " | ♂ 2 " " " " | 1(+1?) | 1(?) | | | | | | | |
| | Total ..... | 5(+1?) | 1(+1?) | | 3 | 1 | | | | |
| ♀ 8 (moderate) | ♂ 1 (normal, of grizzled parentage) | 1 | 1(?) | | | 1 | | 1 | | |
| La J. ♀ 61 (normal, wild) | $C_2$ ♂ 14 (pronounced) | 2(+3?) | 1 | 2 | 2 | 2 | | | | |
| H ♀ 9 " " | $C_2$ ♂ 14 " | | 1 | 2 | 1 | | | | | |
| H ♀ 14 " " | $C_2$ ♂ 14 " | | 1(+2?) | | 1 | | | | | |
| | Total ..... | 2(+3?) | 3(+2?) | 4 | 4 | 2 | | | | |
| La J. ♀ 64 (normal, wild) | ♂ 18 (very pronounced) | 3 | 2(?) | 1 | | | | | | |
| S–P $F_1$ ♀ 3 (normal, unrelated to grizzled) | ♂ 29 (extended A) | 4 | | | | | | | | |
| S–A $F_1$ ♀ 20 " " " " | ♂ 29 " " | | | | | 2 | 1 | | | |
| La J. ♀ 70 (normal, wild) | ♂ 29 " " | 3 | 4(+2?) | 1 | | | | | | |
| La J. ♀ 72 " " | ♂ 29 " " | 4 | 2(+1?) | 2 | 2 | | | | | |
| | Total ..... | 11 | 6(+3?) | 3 | 2 | 2 | 1 | | | |
| ♀ 15 (extended B) | La J. ♂ 30 (normal, wild) | 4 | 1(?) | 2 | 2 | | | | | |
| La J. ♀ 67 (normal, wild) | ♂ 36 (extended C) | 2 | 1 | 5 | 2 | 1 | | | | |
| La J. ♀ 68 " " | ♂ 36 " " | 1 | | 1 | | | | | | |
| La J. ♀ 70 " " | ♂ 37 " " | 2 | 1 | 1 | | | | | | |
| La J. ♀ 67 " " | ♂ 37 " " | 2(+2?) | | | 1 | | | | | |
| | Total ..... | 11(+2?) | 2(+1?) | 9 | 5 | 1 | | | | |

TABLE 1—(*Continued*)

| Mother | Father | Offspring | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Normal (0) | Trace (1) | Slight (2) | Moderate (3) | Pronounced (4) | Very Pronounced (5) | Extended A (6) | Extended B (7) | Extended C (8) |
| A–Y $F_4$ ♀ 16 (albino, unrelated to grizzled) | ♂ 36 (extended C) | | | | | 1 | | | | |
| A–Y $F_4$ ♀ 12 " " " " | ♂ 36 " " | | | | | 1 | | | | |
| | Total ..... | | | | | 2 | | | | |
| ♀ 1 (moderate) | $C_2$ ♂ 14 (pronounced) | | 1 | | | 1 | 1 | | | |
| ♀ 1 " | $C_1$ ♂ 144 " | 1 | 1(+2?) | | 3 | 2 | 1 | 2 | | |
| ♀ 8 " | $C_1$ ♂ 144 " | 1 | 1(?) | | 1 | | | | 1 | |
| | Total ..... | 2 | 2(+3?) | | 4 | 3 | 2 | 2 | 1 | |
| ♀ ? (pronounced or very pronounced) | ♂ 29 (extended A) | | | | 2(?) | 1 | 1 | | | |
| ♀ 47 (very pronounced) | ♂ 58 (pronounced) | | 1 | | | 2 | | | 1 | |
| ♀ 13 (extended A) | ♂ 29 (extended A) | 1 | | 1 | 2 | | 1 | 2 | | |
| | Total ..... | 1 | 1 | 1 | 4 | 3 | 2 | 2 | 1 | |
| ♀ 15 (extended B) | ♂ 18 (very pronounced) | | | | 3 | 1 | | 4 | 1 | 2 |
| ♀ 15 " " | ♂ 29 (extended A) | | | | | | | 1 | 3 | |
| | Total ..... | | | | 3 | 1 | | 5 | 4 | 2 |
| ♀ 38 (extended B) | ♂ 61 (extended B) | | | | | | | 2 | 1 | |
| ♀ 38 " " | ♂ 37 (extended C) | | | | | | | 2 | 2 | 1 |
| | Total ..... | | | | | | | 4 | 3 | 1 |

* In designating the various parents, I have employed the numbers entered in my stock register. Where no prefix is given, the "grizzled stock" series is intended. Mice characterized as "normal, of grizzled parentage" had but a single grizzled parent, except in case of ♀ 40, both of whose parents were grizzled. Those designated as "normal, unrelated to grizzled" are cage-bred stock, having no ancestors nor near kin showing this peculiarity.

The interrogation point after certain numbers indicates the possibility that the individual in question belonged to the next higher class (if 0), or to the next lower class (if 1).

mated with wild individuals or with normal cage-bred individuals unrelated to the grizzled stock.

(2) Every grizzled parent likewise bore (or sired) some non-grizzled offspring. This occurred in most matings of normal × grizzled, and even in some matings of grizzled × grizzled.

(3) In no case, do any of the offspring of wild stock × grizzled display a higher grade of grizzling than the grizzled parent. This is not true, however, in the case of three matings in which "extracted" normals are concerned (*Cf.* foot-note 5).

(4) The mean grade of the progeny is correlated with the mean grade of the parents (Table 2). While no regular order is found among those groups in which one parent is normal, there is a steady increase in the mean rank of the offspring from normal × grizzled matings (collectively considered), through the various types of grizzled × grizzled matings, to ones between mice of the "extended" grades.

TABLE 2*

MEAN GRADE OF GRIZZLING OF OFFSPRING OF EACH TYPE OF MATING

| Grade of parents | Number of matings | Number of offspring | Mean grade of offspring |
|---|---|---|---|
| 0 × 0 (both of grizzled parentage) | 3 | 8 | 0.0 |
| 0 × 1 and 3 (both of grizzled parentage) | 3 | 16 | 1.62 |
| 0 × 4 and 5 (0-parent unrelated to grizzled) | 4 | 26 | 1.42 |
| 0 × 6 " " " | 4 | 28 | 1.21 |
| 0 × 7 and 8 " " " | 7† | 33 | 1.45 |
| 3 × 4 | 3 | 19 | 3.05 |
| (4 to 6) × (4 to 6) | 3 | 15 | 3.73 |
| 7 × 5 and 6 | 2 | 15 | 5.80 |
| 7 × 7 and 8 | 2 | 8 | 6.62 |

* In tabulating these figures, certain groups of matings in the preceding table (*e.g.*, the second and third) have been combined. Likewise, all interrogation points have been disregarded, the doubtful cases being averaged along with the undoubted ones. Such procedure can in no case have introduced an error of more than one grade.

† In two of these seven cases, albino *Peromyscus*, unrelated to the grizzled stock, have been counted as "normals."

(5) All the eight offspring derived from three normal × normal matings (these normals having at least one grizzled parent of high grade) are themselves normal.[4]

One may conclude from the foregoing circumstances, first, that we have to do with a character dependent upon more than one genetic factor, and second, that these factors (or some of them) are dominant, though perhaps incompletely so. I have tried several assumptions respecting the factorial composition of the various grades of "grizzled." Some of these work fairly well for most of the matings, but prove inadequate when applied to others. No thoroughly satisfactory one has been devised. Some reader more adept than I in devising Mendelian formulae might succeed better.

A hypothesis which probably works as well as any other simple one is the assumption that we have to do with two pairs of factors of about equal potency, each incompletely dominant; also that there is a considerable range of variability in the manifestation of each of these factors. Six genotypic grades would be possible from combinations of such assumed factors, *viz.*—gg g′g′, Gg g′g′ (or gg G′g′), GG g′g′ (or gg G′G′), Gg G′g′, GG G′g′ (or Gg G′G′) and GG G′G′. There would obviously be fewer genotypic grades here than there are distinguishable phenotypic ones, but such an assumption would be quite admissible.

I have taken the trouble to put this hypothesis to test in the various types of matings, first assigning an appropriate formula to each of the parents. The greatest discrepancy is in the case of the matings of normals with "extended," B and C, in which the actual proportion of normal and low-grade grizzled offspring is considerably in excess of expectation, even on the assumption that the

[4] However, it would not be surprising if such matings should result in occasional low-grade grizzled. As stated below, it seems likely that some individuals which were assigned to the "normal" class may have been heterozygous for at least one of the (perhaps numerous) factors responsible for this variation.

most extreme grizzled parent was heterozygous for one of these factors.[5]

I attach little importance to such attempted formulations of factorial composition, in the absence of much more extensive data than are here available.[6] They are of interest only as indicating that this general type of explanation is probably applicable to the case in hand. In reality, it is likely that more than two pairs of differential factors (perhaps many) are actually concerned in this case, and that these various factors are not of equal potency. Moreover, a comparison of the offspring of the same grizzled parent by several different normal mates suggests that the latter may carry factors which affect the issue.[7]

In respect to its character and its mode of inheritance, instructive comparisons may be made between the "grizzled" color variation in *Peromyscus* and some other better known cases. The analogy is obvious between "grizzled" and the gray coat color of horses. In each case we have to do with a (wholly or partially) dominant character which does not manifest itself until after at least one molt. And in each case, the eyes and some other parts remain dark. The gray coat in horses is believed, however, to differ from the dark condition by a single factor.[8]

A somewhat closer analogy with grizzled is to be found in the "blaze" of white hairs occasionally met with in human hair, over the center of the forehead.[9] This, also, is a dominant character, not manifesting itself, in some cases at least, until some years after birth, and, furthermore, is restricted to a definite area of the hair. It is, however, regarded as being a monofactorial character,

[5] It would be also necessary to assume that part of the mice with a single dominant factor (*i.e.*, ones with the formula Gg g′g′ or gg G′g′) appear perfectly normal.

[6] I trust that those who may cite this paper will not credit me with a two-factor explanation of the results.

[7] See particularly the offspring of ♂ 29 in table 1.

[8] Wright, 1917; Castle, 1920.

[9] Miller, 1915; Holmes and Schofield, 1917.

though careful investigation might reveal the presence of modifying factors affecting the area.

My own interest in the inheritance of grizzled has been due, in part, to its possible relationship to the inheritance of coat-color in certain natural species and subspecies. Many biologists, particularly taxonomists and field naturalists, have always been impressed by the seemingly sharp contrast between "sports" or "mutations" and the "natural" races of birds and mammals. In the most obvious and familiar cases of color mutation, no graded series exist between the mutant and normal types, such as exist between geographic races, and to a lesser degree between closely related species. In inheritance, also, these two types of variations appear to be radically different, most mutations being inherited in strictly alternative fashion, while racial and specific characters seem to blend or at least to be mixed together inextricably, following a cross.

I was myself much impressed at first—unduly so, as I now believe—by the apparent contrast between these two types of characters. My earlier views on the subject have been shaken, (1) by the observation of cases in which "mutant" characters are not inherited in any simple alternative manner; and (2) by the observation of cases in which subspecific characters tend strongly to segregate after crossing. The second of these classes of phenomena will be discussed in detail in a paper soon to be prepared for publication. The first is well exemplified in the grizzled stock which forms the subject matter of the present paper. In inheritance, the grizzled condition behaves more nearly like some of these subspecific differences, though the resemblance is by no means perfect.

As a further fact of interest, the condition in the more pronounced of these grizzled mice, of the *P. maniculatus* series, bears a considerable resemblance to that of certain individuals of a Florida race, *P. polionotus albifrons*, in which the dorsal surface of the snout and the top of

the head, as far back as the eyes, are white.[10] In the highly modified island race, *P. p. leucocephalus,* this whitening is invariably present and is carried to much greater extremes. In this race, the whole top of the head, as far back as the ears, is often nearly pure white, while the colored parts of the trunk pelage are much paler and grayer than in the (presumably) parent type, *albifrons.* It is likewise of possible significance that in *albifrons* the tail-stripe is commonly vestigial, while in *leucocephalus* it is wanting altogether; also that absence of tail-stripe is incompletely dominant over its presence in crosses with other subspecies.

That the peculiarities of these two subspecies are due, even in part, to the same factors as those which are responsible for the "grizzled" color variation in *P. m. gambelii* is hardly probable, in view of certain important differences between them.[11] But it is of interest to point out this parallelism so far as it goes, since such a situation tends to bridge the gap between "mutations," which arise, or are isolated, under conditions of pedigree breeding, and the characters of "natural" races and species.

*Postscript.*—While this paper was in press, I received from Professor Joseph Grinnell an unusual specimen of *P. maniculatus sonoriensis* from Lower California, near the Colorado River. The specimen has a decidedly whitened face (grade "very pronounced" of my scale) and an imperfect tail stripe. From appearances, I should regard this as an example of the "grizzled" color variation described above for *P. m. gambelii.*

[10] This is the condition which was apparently regarded as typical by Osgood, who first described this subspecies (hence his name *albifrons*). I have found it in only a minority of specimens from any locality, while at some stations it seems to be practically wanting.

[11] For example, the color patterns of *albifrons* and *leucocephalus* are evident in the first coat of hair which is acquired.

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# SYMMETRY IN ORGANISMS

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POSSIBLY the most strikingly symmetrical objects encountered in the natural world are the numerous crystalline forms of minerals. These, together with the similar crystals prepared by the chemist, by evaporation from a concentrated solution or by other means of solidification, are certainly the simplest symmetrical forms of matter. But it is equally obvious that the bodies of plants and animals and their products afford innumerable instances of symmetry, although the manner in which this is exhibited is more complex in most instances, and the range of form of inorganic crystals is altogether transcended. One has only to recall the infinite diversity of leaves, flowers and fruits among the higher plants, of the shells and skeletons of many animals, including those remarkable microscopic organisms belonging to the animal groups of the *Radiolaria* and *Foraminifera,* as well as the more plant-like Desmids and Diatoms. A very slight acquaintance with the varying forms of any of the organic objects mentioned suffices to convince one of the fundamental fact of organic symmetry, and detailed study of any one class of such objects, *e.g.,* flowers, only serves to deepen the impression. Yet surprisingly little is said about it in the current text-books of botany and zoology.

On the other hand, the subject of crystallography, the scientific descriptions of the different kinds of symmetry in crystals, has become an exact science, and the various mineral substances can be grouped into systems, of which six are usually given (18). Not only so, but the underlying basis of crystal form is now known, it being possible to correlate the external form with the molecular structure by means of the X-ray analysis of the substances concerned. In fact, a complete science of the fine

structure of matter—leptology—is being built up as a result of modern physical research.

The most noticeable difference between symmetry in the living and in the non-living is that whereas the latter only involves figures bounded by plane surfaces, the forms of organs and organisms, *i.e.*, of living things and their parts, introduce numerous curved surfaces. This can be correlated with a difference in the state of matter composing the objects in question. Living matter is essentially fluid and colloidal, and in it the forces of surface tension play a very important part. The relation of such forces to the curved surfaces of natural objects has been treated by D'Arcy Thompson (19). It suffices to recall that the sphere is the form assumed by a globule of oil when suspended in an immiscible medium of equal density to itself, and that the spherical form is the starting point of cellular morphology, whilst cell structure underlies all anatomical construction of a higher order. As has been remarked by A. H. Church (3, p. 48), "the approximate cylindrical form of a tree-trunk is but a reflection in the massive soma of the primary claims of surface tension, which gave centric form to the first passively suspended plankton cells."

Most organisms have advanced beyond the spherical state, the symmetry observed being referable to one or more special axes. The position of these imaginary lines and their relations to various planes and points will be referred to later, when it will be found that organic forms can be described by reference to these axes. The existence of such axes, as indicated by structural features, is related to a functional differentiation, possibly referable to a molecular arrangement, or changes of arrangement throughout the protoplasm of the organ or organism concerned. Very little is known as to its exact nature, but of its existence there can be no doubt whatever. The whole phenomenon can be subsumed under the title of polarity, and it presents an undeniable analogy with the phenomena of the electric and magnetic fields. The

structural differentiation of an organ or organism is the most tangible expression of this polarity, but that it has a functional aspect is shown by a simple experiment. It is well known that roots grow downwards, and shoots grow upwards, in response to the force of gravity. It is also well known that a small piece of the stem cut from certain plants will regenerate both roots and leaves. If a short length of stem bearing neither leaves nor stem branches be cut from a plant of the willow genus, *Salix,* and placed in a damp atmosphere, in the course of a few days both roots and leaves will have sprouted from it. The roots always grow downwards, the leaves upwards, but a significant fact can be ascertained by placing pieces of stem in various positions that the leaves always arise from the end of the shoot that was originally uppermost before the piece of stem had been cut out from the complete plant. Similar experiments can be performed with planarian worms where a small length cut out from the body can rejuvenate both head and tail. But the head always arises from the end of the piece which was directed towards the original head of the animal. Certain chemical explanations, as by J. Loeb (12), have been put forward to explain these and other phenomena of regeneration, the differing organs originating in parts of different chemical composition. In this connection the results of C. M. Child (3) are of special interest, as indicating the almost universal occurrence of gradients in intensity of metabolic activity in the protoplasm. It is, therefore, possible to infer as Church (4) has already done in his work on leaf arrangement a molecular protoplasmic basis or correlate for the phenomena of organic symmetry, just as the facts of crystal structure are found to depend or to be correlated with the special features of the fine structure of solids elucidated by means of the Röntgen rays. The different types of organic symmetry can not be understood by isolated consideration of their particular molecular mechanism. It remains to be ascertained why a particular mechanism should exist in one

species and another in a different species, whilst a still other and simpler physico-chemical constitution should be characteristic of non-living matter. Hence the necessity arises for a historical or evolutionary account of living forms.

The starting point for an evolutionary understanding of the phenomena of symmetry must obviously be a classification of the various kinds of symmetry observed. This is, of course, not so easy to obtain as in the case of crystals, which approach much more closely to known geometrical forms. Even the crystal, however, is not mathematically perfect. A. H. Tutton (20) has pointed out that variations of a few seconds of arc occur in the corresponding angles of crystals of one and the same pure substance. Correspondingly with living species there is a somewhat greater variation, amounting to a few minutes of arc between the equivalent angles in crystals of substances which are closely allied, *i.e.*, are capable of forming mixed crystals (20). In view of the fluid and colloidal basis of living bodies we naturally expect a greater divergence from the laws of solid geometry. It is nevertheless surprising how close organisms approximate to certain mathematical figures, and some sort of mathematical treatment is in any case necessary as a means of description.

At an early stage in the history of botany and zoology attempts were made to distinguish the varying forms of the bodies of animals and plants according to their special types of symmetry. It was recognized that the compact bodies of animals, as well as certain parts of plants, such as flowers and fruits, could be divided into types in which the parts were arranged in a radiating manner along a number of axes extending outwards from a center, and those in which the constituents were grouped along a central axis in such a manner that one half was a mirror image of the other. The first type is the well-known radiate symmetry, as exemplied, for instance, in the starfish, while the second is the even more

familiar bilateral symmetry of the human body. In flowers these two main types of symmetry are commonly known as actinomorphic and zygomorphic, respectively.

These symmetry properties were soon requisitioned for the services of classification. In the early part of the nineteenth century it was thought that the natural system of classification might be attained by the use of a limited number of key characters (6). The one character of symmetry was made use of in several early systems in defining primary groups. The best known instance is Cuvier's celebrated classification of the animal kingdom, in which four great groups were distinguished. In three of these the whole animal has a general bilateral symmetry, in the fourth the disposition is radial.[1] Symmetry relationships were also noted by botanists, especially in connection with flowers. The famous Linnean system was partially based on this principle, the number of stamens being the basic character in the arrangement of flowering plants. De Candolle's system even attained many resemblances to the modern grouping, inasmuch as he considered the general symmetry of the plant, an inclusive view, tending towards the modern idea of taking into account the whole organization of each species (6) in order to determine its systematic position. Symmetry must always be of the highest importance of classification and any method of description which would summarize the arrangement of the various parts will be of very great value in this respect. Even the general difference between radial and bilateral symmetry is still used for subdividing the class of the diatoms, which thus fall into two groups, *Centricae* and *Pennatae,* or centric (radial) and pennate (bilateral) diatoms, respectively. The difference between these two types of symmetry in the flower is a valuable distinction between genera and families in flowering plants, and the floral formula is a summarized method of description indicating the actual numbers of members in each whorl of the flower.

[1] Cuvier actually defined the difference on the symmetry of the organs of movement and of sense (7, p. 61).

It is now of course clear that a mathematical arrangement of the forms of symmetry in organisms is something quite distinct from the natural system. Nevertheless, as the latter depends on accuracy of description, the former will form an invaluable weapon in attacking the problem of natural relationship. Thus while the bilateral symmetry of a flower is something different from that of a fish, inasmuch as in classification the character of the symmetry can not be considered apart from the characters of the constituent organs, nevertheless the distinction between bilateral and radial flowers was a big step forward in the history of botany, as it enabled a true comparison between the plan of flowers of related species to be established. For example, without the distinction between actinomorphy and zygomorphy, the relationship between *Ranunculus* and *Delphinium* would have remained hidden, as there would have been no standard of comparison whereby the homology of the two flowers could be traced.

The two main symmetry relations are about the only ones distinguished by modern systematists, many of whom have a deep rooted objection to *thinking* about their work. But other symmetry relations have been distinguished in various ways, at various times, by various authors. For the old nature philosophers the relation of the axis of the body to the center of the earth was important. In the plant the main axis is generally vertical, the plant strives upwards towards the light, and produces its reproductive organs in its uppermost portion. In animals the main axis is generally horizontal, parallel with the surface of the earth. In man the axis of the body again becomes vertical, but the orientation of the body is the reverse of that of the plant. Such comparisons appear meaningless to the modern systematist, who concentrates on differences rather than on resemblances, on analysis rather than synthesis. Some of the early comparisons between the great groups of animals, although made in a manner which is not now considered

legitimate, are of interest as indicating a line of thought which has been too largely neglected within recent years, when morphological comparison, the fundamental basis of an understanding of organic form, has become relegated to a subsidiary place, both in biological research and teaching, to the great detriment of both.

One example of fundamental importance may be given. In Cuvier's system the three phyla of bilaterally symmetrical animals were the *Mollusca,* the *Articulata* and the *Vertebrata.* This appeared in 1817. In 1820, Geoffroy St. Hilaire (8) proposed to include the Articulata of Cuvier in the Vertebrata, under the title of *Dermo-Vertébrés,* the Vertebrata of Cuvier being termed *Hauts-Vertébrés.* In other words, he tried to trace a fundamental similarity between arthropods and vertebrate animals. He regarded each segment of the dermoskeleton of an insect, crustacean or other articulate animal as equivalent to a vertebra. But while in the vertebrate the bulk of the body is on the outside of the vertebra, the reverse is true of the insect or other articulate animal. Every vertebra of the higher animals develops from four centers of ossification. The same is true of the dermovertebrae of lobsters and crabs. The appendages of such animals correspond with the ribs of vertebrates. Geoffroy St. Hilaire went so far as to say that every piece of the skeleton of an insect was homologous with some bone in vertebrates. The interest of this hypothesis from the point of view of organic symmetry is that in order to make the comparison it was necessary to invert the body of the animal. For example, the nervous system of vertebrates is dorsal in position, but in all arthropods it is ventral. Several similar comparisons of vertebrate with invertebrate types have subsequently been made.

The geometrical form of natural objects, especially of organisms, formed the subject of a memoir by H. G. Bronn (2) appearing in 1858. In this the compact form of the animal body was correlated with its sensation and locomotion and distinguished from the elongated form of

the plant, due to its extension in two directions, towards its two sources of nutrition, the sun and the earth. The symmetry of the plant was designated as strobiloid, which indicates, as we shall see later, a kind of spiral arrangement. Three main types of animal symmetry were recognized, and found to correspond with three degrees of motility, *viz.*:

*Amorphozoa:* shapeless: fixed: *e.g.*, Protozoa, sponges.
*Actinozoa:* radiate: (fixed or) moving along any radial axis: *e.g.*, (Coelenterata), Echinoderms.
*Hemisphenozoa:* bilateral: moving along one axis: *e.g.*, all higher animals.

It will be noted that there are transitions between the first two groups, and that the *Actinozoa* really form a link with the plants, although the radiate but not spiral form of these animals distinguished them from the spiral form of most plants.

The classification of organic forms received its most detailed treatment at the hands of Ernst Haeckel (11). His system was a quite general one, suitable alike for the description of the whole organism or any one of its parts down to the single cell. It could even be applied, as its author pointed out to the inorganic realm, and further, to the artificial products of man.[2] The whole system was termed "promorphology" and was intended as a scientific basis for the description and understanding of organic form; in short, of morphology. The scheme is best understood by reference to the various tables given by Haeckel (11), but its scope may be briefly referred to.

Absolutely irregular forms are first enumerated. In these no two diameters are alike, so that no special axis can be distinguished. They are therefore known as *Anaxonia.* Because they do not possess a special center they are also spoken of as *Acentra.* Their ground form is the bolus, and they are illustrated by the whole body of many amoebae and sponges. All other forms are referred to as *Axonia,* and are classified by means of the special axes which may be distinguished in them, owing

[2] And, one may add, of animals, *e.g.*, the nests of birds.

to the structural equivalence of the various parts. The simplest forms of these have a number of equal axes. Their ground forms are the sphere and the endosphaeric polyhedron, the former being illustrated by examples from radiolarian cells, and simple colonies like *Volvox,* the latter also from radiolarian cells, from pollen grains, and the antheridia of *Chara.* In all these a central point can be distinguished, and they are called *Centrostigma.* There is a third group of forms, radially symmetrical around a central axis, and hence known as *Centraxonia.* The ground forms of this group include the sphaeroid, cylinder, ovoid, cone, and some forms of pyramid and double-pyramid. It will be noted that this group includes some figures in which the longitudinal axis has similar poles, such as the sphaeroid illustrated by the radiolarian *Coccodiscus,* and others, like the cone seen in the foraminifer *Conulina,* have poles which are dissimilar. The double-pyramid may be contrasted with the pyramid in this respect. These forms can be illustrated by the bodies of various protozoa, whilst the figures showing polar differentiation are also typical of many flowers and medusae. The pyramids and double pyramids included in this group are those which possess a base which is completely radially symmetric, or one which can be divided, such as the rhomb, into two equal parts by more than one line of division. In other words, there is no polar differentiation of a dorso-ventral axis. But in a fourth group, including the most familiar bilateral types, such as the bodies of most vertebrates, not only is the ground form pyramidal, thus showing polar differentiation of the longitudinal axis, but a dorso-ventral axis is also differentiated, owing to the difference between the dorsal and ventral surfaces of the body. These exhibit symmetry about a central plane, and are hence known as *Centroplana.* In most of these, as in the human form, the two sides of the body are externally alike, but in a few, as in the flat fishes, lateral differentiation is also obvious. This group also includes the form of some zygomorphic flowers.

The possibility of a system of promorphology depends upon the fact that organisms are so constructed that it is possible to compare one part with another. It is merely a logical extension from the facts of bilateral and meristic homology, *i.e.,* of homology within a single organism. Organs or parts may be comparable without their figures being capable of geometrical superposition. This is obvious in the comparison of the corresponding parts of different organisms, and is capable of geometrical treatment (see 19). Lateral differentiation has already been referred to, and it must not be supposed that organisms showing differentiation in the three planes of space are necessarily comparable with the anaxial types. The axes are defined by comparable parts, which may, however, not be identical in form.

Parts of organs may also be symmetrical in some respects, but not in others. Most of the examples given in Haeckel's system refer to the external form of organisms, organs or parts. *Volvox,* for example, is cited as a sphere. From the point of view of the internal structure it might be classed as a polygon, each cell surface forming one face. In the same way the human body, although forming an excellent example of bilateral symmetry, might come under the category of the laterally differentiated, if some of the internal organs were alone considered. The asymmetry of the human skull, in certain dimensions, has been established by D. Hepburn (12). Even the normal human spine is probably asymmetrical, in fact slightly spiral in form. The difference in right and left limbs is well marked.

Haeckel's scheme is applicable to all plant and animal organs but is most readily appreciated by reference to organs of limited growth. The straggling forms of plants introduce the need for a further analysis of the problem. The ordinary green shoot of a plant is a radially symmetrical structure, based on a cylindrical or conical ground form. But owing to its relatively great elongation, and rhythmic repetition of leaf bearing points

or nodes the differentiation of the longitudinal axis becomes a complicated matter. The nodes are not all the same distance apart, and the spatial relations which exist between them exhibit characteristic differences, as has been shown by P. Groom in various plant families (9) and in detail in *Centrospermae* (10).

Whilst the animal body generally grows in all its parts at the same time, the plant, apart from any radial increase, is actually adding new organs in series at its growing point. These two methods of growth, although on the whole distinctive of plants and animals respectively, are not absolutely separated. Even in the vertebrates a faint approach to the plant-like method is seen in the adding on of segments during the stage in embryonic development when the number of segments is being increased. And in the growth of shells an analogous adding on of material takes place. It is the addition of new parts or organs, in cases of continued growth of this kind, that entails the necessity for further analysis of the problem of symmetry.

Imagine a cylinder and a cone. Material is added on at the base of each cone of these figures and the cylinder or cone increases in height. This is the simplest method of growth. The primitive molluscan univalve shell was a low cone which, as it increased in height, inclined to one side of the animal with the result that additional material was added on to the other. The plant stem increases after the model of the cylinder, material being added from above. The leaves are added as an investment around the stem. If this investment took the simplest theoretical shape it would have the ground form of a regular cylinder. The leaves would then form a series of circles (*i.e.*, the whorls) around the stem and would then be so arranged that the members of one whorl would be then immediately below those of the next. This arrangement is very rare. This formation of alternating whorls is commoner, and leads over to the more frequent condition in which the leaf arrangement is completely

spiral. The ordinary condition depends on the addition of new material, in the form of a single leaf primordium to one side of the growing point. As in the case of the spiral shell, the leaf spiral depends on the asymmetrical addition of new material. If, however, the leaves continued to be formed at one point at the side of the growing point a helix could not be formed. The latter depends on a balancing effect of successive leaves, each leaf added to the system tending to balance the leaves already formed. Thus the system as a whole remains radially symmetrical, although the individual leaves are added asymmetrically, *i.e.*, laterally.

In plants the spiral is thus actually a helix because upward growth is combined with lateral increase. In *Foraminifera* the spiral formed by successive chambers of the animals is in a single plane. The shell has a bilateral symmetry in this plane. In *Mollusca* both helical (turbinated) and plane spiral (discoid) forms occur. The development of a helical from a discoid shell is probably associated, it is suggested by Shipley and MacBride (17), with the crawling habit. For the only existing *Mollusca* possessing large coiled shells and yet retaining bilateral symmetry are swimming Cephalopods, belonging to the genera *Nautilus* and *Spirula.*

In 1838, Canon H. Moseley (see 5) communicated to the Royal Society of London his discovery that the figure of the turbinated and discoid shells of molluscs was that generated by the revolution, about the shell axis, of a curve which continually varied its dimensions according to the law of the logarithmic spiral. Goodsir continued this work and pointed out that the logarithmic law of increase must be the law of growth (5). Of course growth is equally well expressed by the straight line and circle, but these are only limiting cases of the logarithmic spiral. The latter is thus the absolutely generalized expression of growth. From it we can predict the position of the future organs or parts formed in a spiral organism just as our knowledge of the law of gravitation enables us to

predict the future position of the planets. Goodsir pointed out, in fact, a very close analogy between the law of attraction and the law of production or growth. It will be remembered that Newton, in his *Principia,* showed that gravitational attraction varies inversely as the square of the distance, and that the fact that the planets revolve in ellipses depends on this fact. Newton had also pointed out that if attraction had varied as the inverse cube of the distance the heavenly bodies as Sir Theodore Cook (5) expresses it "would not have revolved in ellipses but would have rushed off into space in logarithmic spirals." Goodsir therefore regarded the law of the cube as the law of growth, just as the law of the square is the law of attraction (5). He connected it with the three-dimensional form of the cell (5). The principle of the orthogonal construction of the cell (*i.e.,* the tendency of cells to produce new walls at right angles to those already present) was insisted on by the botanist Sachs (15). More recently the principle of orthogonal segmentation has been applied to the formation of leaf primordia at the apex of the plant shoot, quite apart from the constituent cells, by A. H. Church (4).

Unfortunately the ideas of Goodsir have never been properly followed up, but some further light on the subject of spiral growth may be obtained through a knowledge of leaf-arrangement. This subject, like so many other scientific problems, had interested Leonardo da Vinci at the beginning of the sixteenth century. He says (*Inst. de France,* translation quoted from Cook):

> Leaves in their earliest growth turn themselves round towards the branch in such a way that the first leaf above grows over the sixth leaf below: and the manner of their turning is that one turns towards its fellow on the right, the other to the left.

In another passage (*loc. cit.*) he speaks as follows:

> The leaf always turns its upper side towards the sky so that it may be better able to receive the dew over its whole surface; and these leaves are arranged on the plants in such a way that one covers another as little as possible. This alternation provides open spaces through which the sun and air may penetrate. The arrangement is such that drops from the first leaf fall on the fourth leaf in some cases and on the sixth in others.

Da Vinci thus recognized two principles which have in modern times been the basis of the subject of phyllotaxis, as it is now called. The first of these was the idea of tracing the spiral of leaves up or down the stem until another leaf immediately above or below it was found. The botanists of the early nineteenth century found this a convenient way of marking out the position of the leaves on the "genetic spiral" as the helix, formed by imaginary joining up of the bases of the leaves around the stem, was called. And here it may be noted that phyllotaxis is concerned only with the position of the points on the stem at which the leaves are inserted. Secondary changes in the forms or positions of the leaves do occur, and sometimes make it very difficult to determine this primary arrangement. Thus (i) a leaf may become dissected to let the light through; (ii) the internodes between the leaves may elongate, a process that may be modelled by the drawing out of a telescope; (iii) the leaf stalks may become elongated; (iv) the main stem may become twisted; (v) the leaf stalks may become twisted. All this has nothing to do with the primary arrangement of the leaves, with which we are alone concerned.

Bonnet (1) thought that in studying the genetic spiral he could start with the point of insertion of one leaf and find another directly above it. Da Vinci seems almost to have implied this, although it is, in fact, in contradiction to his second principle, that the leaf arrangement is that which secures maximum illumination. The whole of the earlier work on phyllotaxis, however, was based on the assumption that one leaf was inserted immediately about another.

Bonnet (1) distinguished five types of leaf arrangement: (i) whorled, *i.e.,* more than one leaf at a single node; (ii) alternating, *i.e.,* two longitudinal rows, not whorled; (iii) decussate, *i.e.,* four longitudinal rows, not whorled; (iv) quincuncial, *i.e.,* the sixth leaf immediately above the first, the genetic spiral passing twice around the stem between the first and sixth; (v) multiple spirals.

Shortly afterwards Schimper and Braun (16) introduced an essentially similar, although clearer system, which is still described in the text-books. Vertical lines, joining leaves which are inserted one immediately above the other, or superposed, as we may say, are known as orthostiches. Spiral lines, passing obliquely from one leaf to the next on the stem, are called parastiches. Schimper and Braun expressed the phyllotaxis, or leaf arrangement of a particular plant, by a fraction, the denominator of which was obtained by counting the number of leaves from any given one to the next superposed above it. Thus if we label a given leaf 1 and the next on the spiral 2 and so on, then if the leaf numbered 6 is on the next leaf superposed to 1, then five leaves have been encountered in passing from 1 to 6. The denominator in the formula for this form of leaf arrangement is then 5. The numerator is obtained by counting the number of times the spiral along which the leaves are placed—the genetic spiral—passes around the circumference of the stem before another leaf immediately above the first leaf is encountered. This may be 2. In such a case the genetic spiral crosses the vertical line—the orthostichy—joining the first and sixth leaves once, but does not bear a leaf at this point.

The phyllotaxis formula has been worked out in this way for a number of cases and the fact emerges that the number of leaves from one superposed member to the next is generally one of the numbers

$$1, 2, 3, 5, 8, 13 \ldots\ldots$$

This series is usually stated to have been first recognized by an Italian mathematician, Leonardo da Pisa or Fibonacci, in the thirteenth century. It is, therefore, usually called the Fibonacci series. Kepler (see 14), however, knew of these numbers and of their expression in natural objects. The series has the property that the ratio of any two adjacent members of the series is approximately constant, and continually approaches more closely to the exact value of $\frac{\sqrt{5}-1}{2}$ as we ascend

the series. Now it happens that the phyllotaxis arrangements, resulting from this, show angles which closely approach what has been termed the "ideal angle" (see 4), *viz.*, that at which there will be minimum superposition. This was first calculated by Bravais (see 4) and is found to be

$$137° \ 30' \ 28.936''$$

Now consider the angles given by the most common phyllotaxis arrangements as measured by the Schimper and Braun scheme:

$$\tfrac{2}{5} \text{ of } 360° = 144°$$
$$\tfrac{3}{8} \text{ of } 360° = 135°$$
$$\tfrac{5}{13} \text{ of } 360° = 138° \ 27' \ 41.54''$$

The most recent work on phyllotaxis includes that of A. H. Church (4), which must briefly be referred to here. Church adopted the method of plotting the whole three-dimensional system in two dimensions, the projection having no effect whatever on the angles of divergence between the leaves. When the Schimper-Braun system is projected in this way the leaves are found to be arranged in a spiral of Archimedes. Unlike previous authors, who had confined their attention to the adult part of the plant, Church made an examination of the growing apex of the plant. He found in plants which had been ascribed such phyllotaxis formulae as given above, *viz.*, $\frac{2}{5}$, $\frac{3}{8}$ and $\frac{5}{13}$, no evidence whatever that one leaf is ever exactly superposed to another. In fact, as far as actual measurements go the ideal angle was even more closely approached than those given by the Schimper-Braun scheme. In normal cases the diagrams of leaf-primordia[3] obtained by Church's method will show the primordia to be arranged in such a way that they lie on two sets of spiral curves which cut one another. These curves are logarithmic spirals. The supposed orthostiches, joining leaves alleged to be immediately above

[3] Primordium is a useful botanical term for the first appearing portion of a part or organ. This might very well be adopted by English zoologists who have no suitable equivalent for what their German colleagues call *Anlage*.

one another, do not exist in plants, which show a leaf divergence near the ideal angle. The apparent observation of superposition is due to the difficulty of measuring the exact points of insertion of leaves in the adult shoots where they are separated by internodes. The true arrangement is best observed in growing points and other compact structures. The individual scales of Pine cones can generally be seen arranged along two sets of spirals, of which there are usually eight ascending the cone in one direction and five, crossing them, ascending in the opposite direction. In a larger cone one may find eight crossing thirteen. The same phenomenon may be easily seen in the flower heads of many *Compositae,* since each flower occurs at a node[4] and the flowers are crowded together. In the heads of *Centaurea,* for example, the units may be arranged in a series of 34 spirals crossing an opposing set of 55, and even the larger numbers 89 and 144 are not infrequently met with. The ideal angle thus is still an expression of the Fibonacci series, however, although the numbers appear in ratios, not in fractions. The formula is simply the ratio of the number of spirals in each direction required to show the positions of the leaves: $m + n$ or better $m : n$. $M$ and $n$ are found in practice to be Fibonacci numbers. The angles of divergence obtained by plotting the points of leaf insertion on this system, and which should be compared with those given by the older system, are as follows:

$2 + 3 = 138° \ 27' \ 42''$
$3 + 5 = 137° \ 38' \ 50''$
$5 + 8 = 137° \ 31' \ 41''$

When m = n the construction is symmetrical, the more usual asymmetrical or spiral arrangement occurring when m and n are unequal. The symmetrical construction is that long known in botany as whorled phyllotaxis, in which members of successive whorls alternate. Superposed symmetrical constructions are exceedingly rare

[4] A study of leaf arrangement in higher plants is also a study of branch arrangement since each branch arises in the axil of a leaf, or where a leaf once occurred either in ontogenesis or phylogenesis.

and in all cases show evidence of being derived from other types. All symmetrical systems would appear to have been derived from the spiral, in fact, as suggested by the alternation of whorls in most symmetrical forms. Asymmetrical phyllotaxis with no common factor for $m$ and $n$ is the commonest case. Here one grand spiral will pass through all the points of intersection.

Church calls all the spirals of such a system parastiches, of which the orthostiches which do occur in whorled symmetrical constructions are only a special case. He calls the primary curves of the system contact parastiches. Every form of phyllotaxis which is rhythmic, *i.e.*, which forms a pattern, is readily expressible in terms of such curves and in no other manner. The figures formed by the intersection of the two sets of curves are called quasi-squares, and the curves that can be inscribed in the latter are termed quasi-circles. The mathematical properties of the quasi-circles afford an illuminative explanation of all the essential and primary attributes of a leaf. The older morphologists knew that a leaf had the three fundamental properties of (i) bilaterality, (ii) dorsiventrality, (iii) isophylly. That all leaf-primordia necessarily present these essential attributes follows directly from the logarithmic spiral construction postulated by Church, and not from any other construction. Finally Church's theory is based on the assumption of an equal distribution of growth energy around the growing point, as is justified from its radial construction.

The logarithmic spiral theory of phyllotaxis, or as its author prefers to call it the equipotential theory, thus appears to fit the facts, and explains more than the old theory based on the spiral of Archimedes. Church has found it not only in higher plants but also in seaweeds. The logarithmic spiral is also the nearest common mathematical expression one can find for the form of the numerous spiral species of Molluscs. The same curve is the basic line of development for the Foraminifera. It is clearly exhibited, in fact, as D'Arcy Thompson has

pointed out (19) whenever parts of different age are present. Curiously enough the same form also appears in many works of art.

The so-called "Golden Mean" is a proportion 1: $\frac{\sqrt{5}-1}{2}$ obtained by dividing a line in such a manner that the ratio of the lesser portion of the line to the greater is equal to the ratio of the greater portion to the whole line. This proportion, which appears to rule the construction of a vast number of natural structures as well as objects of art, has been known from early times, and is the basis of a mathematical series to the members of which the Fibonacci numbers are the nearest approximation in integers.

No object of nature or art is ever mathematically perfect. In fact, one may agree with Sir Theodore Cook (5) that perfection in nature and art depends on slight, often almost imperceptible divergence from the mathematical expression, however subtle. Enough has been said to prove that, nevertheless, the principle of symmetry is a fertile conception and a powerful weapon in the analysis of organic form. The subject could be extended indefinitely. A great number of topics might equally well be correlated with what has preceded. The rather important subject of twins, for example, is largely a matter of symmetry, and the laws of Mendelism are a question of symmetrical relationships between individuals. All these facts could be correlated and would then throw light upon one another. It is evident, therefore, that the widespread recognition of symmetry as a synthetic principle would give an enormous impetus to the progress of the biological sciences.

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# GLOSSY SEEDLINGS IN MAIZE[1]

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THE importance of further studies of linkage relations with other organisms than Drosophila is recognized generally by students of genetics. Extensive investigations have been made with maize and eight groups of linked factors have been determined (see Hayes and Garber, 1927). Many studies of the inheritance of maize characters have been made for the purpose of obtaining new characters which can be used to advantage in linkage studies.

Seed and seedling characters which can be differentiated without growing the plants to maturity are especially valuable. A recessive character called "glossy seedling" has been studied by Kvakan (1924) and Brunson (1926). It can be differentiated easily in the seedling condition after a little practice. The character expresses itself as a glossy or waxy appearance of the under and upper surfaces of the leaves of maize seedlings. Counts of normal and glossy seedlings are facilitated by sprinkling the seedlings with water. The normal seedlings shed water almost completely, while the glossy seedlings retain drops on the surface of the leaf. Such a procedure is necessary in order readily to distinguish between normal and glossy in white or yellow seedlings. The glossy seedling studied by Kvakan and Brunson is a simple recessive to normal and the factor concerned has been located in one of the linkage groups together with factors for brown aleurone and ramose plant. Preliminary studies have been reported of other characters which are also dependent upon factors belonging to this same linkage group (Hayes and Brewbaker, 1926). One of these slashed, a seedling character recessive to normal, has

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been studied extensively by the junior author, who has obtained sufficient data to lead to the conclusion that the factors located in this chromosome pair are independent in inheritance of those which are found in the other seven linked groups of factors. This study will be reported in a separate paper.

Glossy seedlings have been found rather frequently in many varieties and selfed lines of maize which have been used in breeding studies at Minnesota. Intercrosses between glossy seedlings isolated in the same or different varieties have been made to determine whether all glossy seedlings were dependent upon the same or different factors. A summary of the intercrosses which have been made between fourteen strains pure for glossy seedlings is given in Table 1.

TABLE 1

INTERCROSSES OF GLOSSY SEEDLING STRAINS

| | Varieties | $gl_1$ | | | | | | | $gl_2$ | | | | $gl_3$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| | 1 | ... | gl | gl | gl | gl | gl | ... | N | N | N | N | N | ... | N |
| | 2 | gl | ... | gl | gl | gl | ... | ... | N | N | N | N | N | ... | N |
| | 3 | gl | gl | ... | gl | gl | ... | gl | N | N | N | N | N | N | ... |
| $gl_1$ | 4 | gl | gl | gl | ... | gl | gl | gl | N | N | N | N | N | N | N |
| | 5 | gl | gl | gl | gl | ... | gl | gl | N | N | ... | N | N | N | N |
| | 6 | gl | ... | ... | gl | gl | ... | ... | N | ... | ... | ... | ... | ... | N |
| | 7 | ... | ... | gl | gl | gl | ... | ... | ... | N | ... | N | N | N | N |
| | 8 | N | N | N | N | N | N | ... | ... | gl | gl | gl | N | N | N |
| | 9 | N | N | N | N | N | ... | N | gl | ... | gl | gl | N | N | N |
| $gl_2$ | 10 | N | N | N | N | ... | ... | ... | gl | gl | ... | ... | N | ... | ... |
| | 11 | N | N | N | N | N | ... | N | gl | gl | ... | ... | N | ... | N |
| | 12 | N | N | N | N | N | ... | N | N | N | N | N | ... | gl | ... |
| $gl_3$ | 13 | ... | ... | N | N | N | ... | N | N | N | ... | ... | gl | ... | gl[1] |
| | 14 | N | N | ... | N | N | N | N | N | N | ... | N | ... | gl[1] | ... |

[1] Only one seedling was obtained.

*Varieties used:*

1. Brunson's $gl_1$.
2. Rustler.
3. Northwestern Dent.
4. (69–6) × (1–6).
5. King Phillip.
6. Silver King.
7. Country Gentleman.
8. Longfellow.
9. Crosby.
10. Squaw.
11. Manitoba Flint.
12. Minn. No. 23.
13. Michigan Pop.
14. Lancaster Sure Crop.

In Table 1 the crosses which gave normal seedlings are noted by N, while the glossy seedlings are designated by gl. The data given prove that there are three genetically different glossy seedlings, and these are designated as $gl_1$, $gl_2$, $gl_3$. The glossy called $gl_1$ is the same as that studied by Brunson and Kvakan. The strain of Lancaster Sure Crop is probably $gl_3$, although the data obtained were not sufficient to prove this conclusively. Only one seedling of a cross of this strain with Michigan Pop was obtained and this one was glossy.

Summarized $F_2$ data from intercrosses of $gl_1$, $gl_2$ and $gl_3$ are given in Table 2.

TABLE 2

SEGREGATION FOR GLOSSY SEEDLINGS IN THE $F_2$ GENERATION OF INTERCROSSES BETWEEN $GL_1$, $GL_2$ AND $GL_3$.

| Cross | Normal | Glossy | Dev. in Nos. from 9:7 | P. E. numbers | Dev. / P. E. |
|---|---|---|---|---|---|
| $gl_1 \times gl_2$ ..... | 11623 | 8672 | 207.1 | 47.7 | 4.3 |
| $gl_1 \times gl_3$ ..... | 2340 | 1861 | 23.1 | 21.7 | 1.1 |
| $gl_2 \times gl_3$ ..... | 1222 | 980 | 16.6 | 15.7 | 1.1 |

The $F_1$ of intercrosses between $gl_1$, $gl_2$ and $gl_3$ were normal, and in $F_2$ there was a close approach to a 9:7 ratio of normal *vs.* glossy in the crosses of $gl_1 \times gl_3$ and $gl_2 \times gl_3$. In the cross of $gl_1$ with $gl_2$ the deviation from a 9:7 ratio was larger than would be expected normally on the basis of random sampling.

Crosses between $gl_2$ and factors in each of the eight linkage groups have been made and linkage relations with endosperm characters have been determined. The $gl_2$ strains used in these studies were a Longfellow flint strain characterized by Yellow flinty seeds and Crosby sweet, a white wrinkled seeded variety. The relation of $gl_2$ to the aleurone color factors A, C and R is given in Table 3. The value of p or crossing over expressed as a decimal fraction is calculated from a formula given by Collins for 3:1 and 9:7 ratios when complementary factors are concerned and by Yule's coefficient of association

when the aleurone color segregation is dependent only upon a single factor pair (see Table 3).

TABLE 3

RELATION OF C, R AND A TO $gl_2$ IN CROSSES OF AA CC RR $gl_2$ $gl_2$ WITH ALEURONE TESTERS OR PURPLE ALEURONE STRAINS. $F_2$ DATA.

| Culture No. | Heterozygous for | Colored $Gl_2$ | Colored $gl_2$ | Colorless $Gl_2$ | Colorless $gl_2$ | Total | Calculated p[2] |
|---|---|---|---|---|---|---|---|
| 167..... | Rr | 1517 | 514 | 662 | 233 | 2926 | .4947 |
| 171..... | Rr | 1152 | 412 | 503 | 141 | 2208 | .5342 |
| 176..... | Rr | 1049 | 390 | 331 | 135 | 1905 | .4867 |
| 170..... | Cc and Rr | 1045 | 388 | 783 | 275 | 2491 | .4964 |
| 173..... | Cc and Rr | 730 | 236 | 568 | 216 | 1750 | .5243 |
| 179..... | Cc and Rr | 755 | 251 | 541 | 187 | 1734 | .5310 |
| 169..... | Aa and Rr | 916 | 294 | 709 | 228 | 2147 | .5042 |

[2] The value of p for the linkage relation of $gl_2$ in relation to R was calculated for the coupling phase, and in relation to C and A where 9:7 ratios were involved for the repulsion phase.

The results indicate that the factor pair $Gl_2$ $gl_2$ is independent in inheritance of the three aleurone color factors A, C and R.

The factors for waxy and shrunken seeds are located in the same linkage group as the C aleurone factor. $F_2$ data regarding $gl_2$ and wx are given for a cross of Wx Wx $gl_2$ $gl_2$ with wx wx $Gl_2$ $Gl_2$. The results compared with expectation on the basis of a 9:3:3:1 ratio are as follows:

| Wx $Gl_2$ | Wx $gl_2$ | wx $Gl_2$ | wx $gl_2$ | Total | $X^2 = 1.96$ |
|---|---|---|---|---|---|
| 1646 | 573 | 533 | 174 | 2926 | P = .5816 |

In a similar cross the data for the relation of shrunken and glossy were as follows:

| Sh $Gl_2$ | Sh $gl_2$ | sh $Gl_2$ | sh $gl_2$ | Total | $X^2 = 10.77$ |
|---|---|---|---|---|---|
| 1281 | 439 | 374 | 114 | 2208 | P = .0143 |

The results indicate that the factor pair $Gl_2$ $gl_2$ is independent in inheritance of C, wx and sh which belong to the linkage group commonly designated as the "C" group. The low value of P for the relation of $Gl_2$ $gl_2$ to Sh sh is due mainly to the lower germination of shrunken

seeds. A calculated C. O. value of 48.39 per cent. was obtained by the use of Yule's Coefficient of Association.

Studies of the inheritance of $gl_2$ in relation to the Su su factor pair were obtained for both the coupling and repulsion phases. The repulsion phases were obtained from Longfellow crosses and the coupling phases from Crosby crosses. Data are given in Table 4 with p calculated as a decimal fraction by the use of Yule's Coefficient of Association.

TABLE 4

RELATION OF SU SU AND $Gl_2$ $gl_2$ IN CROSSES OF SU $gl_2$ WITH SU $Gl_2$ AND RECIPROCAL

| Culture No. | Relation | Starchy $Gl_2$ | Starchy $gl_2$ | Sugary $Gl_2$ | Sugary $gl_2$ | Total | p |
|---|---|---|---|---|---|---|---|
| 170 | Repulsion | 1064 | 412 | 328 | 100 | 1904 | .4660 |
| 173 | Repulsion | 1015 | 340 | 283 | 112 | 1750 | .5177 |
| 176 | Coupling | 1080 | 413 | 300 | 112 | 1905 | .5042 |
| 179 | Coupling | 518 | 181 | 148 | 53 | 900 | .4980 |

Apparently $gl_2$ is independent of the factor pair for normal *vs.* sugary seeds.

The crosses with Longfellow glossy gave an opportunity to study the inheritance of $Gl_2$ $gl_2$ in relation to the factor for yellow endosperm carried by the Longfellow parent. Data are given in Table 5 and p is calculated from Yule's Coefficient of Association.

TABLE 5

RELATION OF YY TO $Gl_2$ $gl_2$ IN $F_2$ CROSSES

| Culture No. | Relation | $YGl_2$ | $Ygl_2$ | $yGl_2$ | $ygl_2$ | p |
|---|---|---|---|---|---|---|
| 169 | Repulsion | 525 | 166 | 184 | 62 | |
| 170 | " | 583 | 209 | 200 | 66 | |
| 171 | " | 394 | 111 | 109 | 30 | |
| 168 | " | 654 | 215 | 230 | 87 | |
| | Total | 2156 | 701 | 723 | 245 | .5060 |

The results indicate independent inheritance for Yy and $Gl_2$ $gl_2$.

Possible linkage relations were studied for $Gl_2$ $gl_2$ and the factor pair which differentiates flinty *vs.* floury seeds. Flinty *vs.* floury segregates in $F_2$ in a ratio of 1:1 (Hayes and East, 1915). $F_2$ data from a cross of pure glossy, $gl_2$ from Longfellow flint corn with a floury non-glossy race are given in Table 6.

TABLE 6

LINKAGE BETWEEN FLINTY-FLOURY *vs.* $Gl_2$ $gl_2$ IN CROSSES OF FLINTY $gl_2$ $gl_2$ WITH FLOURY $Gl_2$ $Gl_2$. $F_2$ DATA.

| Ear No. | Flinty | | Floury | |
|---|---|---|---|---|
| | $Gl_2$ | $gl_2$ | $Gl_2$ | $gl_2$ |
| H 168–1 | 84 | 24 | 94 | 15 |
| –2 | 63 | 30 | 63 | 13 |
| –3 | 93 | 51 | 105 | 18 |
| –4 | 69 | 47 | 119 | 19 |
| –5 | 78 | 57 | 116 | 28 |
| Total ..... | 387 | 209 | 497 | 93 |

The linkage value was calculated from the formula given by Collins (1924) where $p = \frac{2(Ab + aB)}{n} - .5$, and Ab and aB contain the new combinations of parental characters. The calculated value of p expressed as a decimal fraction was .309.

From the cross of sugary $gl_2$ (Crosby) with floury $Gl_2$ the following results were obtained:

| Flinty | | Floury | | Sugary | |
|---|---|---|---|---|---|
| $Gl_2$ | $gl_2$ | $Gl_2$ | $gl_2$ | $Gl_2$ | $gl_2$ |
| 299 | 177 | 346 | 52 | 194 | 46 |

The calculated value of p by the use of the coefficient of association for the linkage relation of Su su and $Gl_2$ $gl_2$ was .5568. Using only the starchy seeds, a calculated value of the linkage relation for flinty-floury *vs.* $Gl_2$ $gl_2$ was .303, which was very similar to that from the previous cross.

One ear of a cross of Ramose floury seeds with $gl_2$ in Longfellow flint was studied. Results were as follows:

| Flinty | | Floury | |
|---|---|---|---|
| $Gl_2$ | $gl_2$ | $Gl_2$ | $gl_2$ |
| 85 | 43 | 109 | 23 |

A calculated linkage value of p = .331 was obtained.

This is the first reported linkage relation of the flinty-floury endosperm factor pair with any other factor pair. Several studies of the relation of flinty-floury with other characters have been made and others are under way. These will not be reported in detail in this paper.

From $F_2$ data flinty-floury appear independent in inheritance of the following factor pairs which are in known linkage groups.

Yy , yellow *vs.* colorless endosperm
Gl, $gl_1$, normal *vs.* glossy seedling
Sl sl , normal *vs.* slashed seedling
Gg , normal *vs.* golden plant
Ra ra, normal *vs.* ramose plant.

Flinty-floury also appears independent in inheritance of the following characters which have not been located in any linkage group:

(1) A recessive virescent seedling in Minn. No. 13 which grows to maturity. From $F_2$ data it appears that this character is not closely linked with any of the known linkage groups.
(2) Sorghum tassel, a recessive character, which has been studied in $F_2$ and which does not show close linkage with any known linkage group.
(3) Brown midrib, a recessive character, which has been studied rather extensively at Minnesota without finding a linkage with any known linkage group.

## SUMMARY

(1) In addition to the glossy seedling located in the linkage group Bn-sl-$gl_1$-ra two new glossy seedlings have been discovered. The three glossies are designated as $gl_1$, $gl_2$ and $gl_3$.

(2) Intercrosses of $gl_1$, $gl_2$ and $gl_3$ give normal seedlings in $F_1$ and a ratio of 9 normal to 7 glossy in $F_2$.

(3) $Gl_2$ appears independent in inheritance of the aleurone factor pairs Cc, Rr and Aa, and of the endosperm factors Wx wx, Sh sh, Su su and Yy.

(4) $Gl_2$ is linked with the factor pair for flinty *vs.* floury endosperm with a recombination percentage of about 30.

(5) A summary statement is included which indicates that flinty *vs.* floury is independent in inheritance with the following factor pairs where the position in the chromosome map is known, namely, Yy, $Gl_1$ $gl_1$, Sl sl, Gg, Ra ra. The flinty-floury factor pair gave independent inheritance also with factor pairs for Minn. No. 13 virescent seedling *vs.* normal, sorghum tassel *vs.* normal and brown midrib *vs.* normal, which have been studied extensively with known linkage groups without finding a close linkage relation.

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# THE HABITATS OF PLETHODONTIDAE[1]

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MY monograph of "The Salamanders of the Family Plethodontidae" was published in 1926. Two papers by Dr. G. K. Noble, dealing with some of the matters considered therein, appeared, one in 1925, too late for its conclusions to receive due consideration in my monograph, and one in 1927. I find it necessary to consider his remarks, since our views do not wholly coincide, and it is best to set down the divergence of opinion, lest my silence should, erroneously, convey the impression of concurrence.

In 1899 Lönnberg suggested that the absence of the lungs and of the hydrostatic mechanism connected with them is correlated with peculiar aquatic habits, since these forms are in large part inhabitants of running water, in which these organs would be unnecessary or even disadvantageous. Mrs. Wilder (1906) emphasized by her work on the ypsiloid apparatus the special hydrostatic function of the lungs in connection with this apparatus. In 1920 Mrs. Wilder and myself put forward the suggestion that such hydrostatic organs are worse than useless to animals living in current. We supported our statements by observations of behavior of lunged and lungless forms in current and in still water, and added a list of salamanders of various families, all with lungs in varying degrees of degeneration and all with habitats, according to authors, in or near mountain streams.

Before our paper of 1920 some other explanations had been offered. Camerano[2] advanced a theory, which was quoted with approval by Boulenger (1910, p. 33), who says:

[1] Contributions from the Department of Zoology, Smith College, No. 149.

[2] 1894, Atti. Acc. Sc. Torino 29, p. 705, and 1896, 33, p. 512.

> It is probable, as Camerano has remarked, that terrestrial life has brought about a reduction of the lungs, whose hydrostatic function is manifest in aquatic species; these lungs, very simple in structure, not sufficing any more for aerial respiration, so that this is supplemented by the bucco-pharyngeal cavity, which acquires more and more the respiratory faculty until the lungs become superfluous and fall into desuetude. . . .

The aquatic lungless forms "descend from ancestors become terrestrial and having in consequence lost the lungs" and are unable to regain them. This is contradicted by such terrestrial lunged forms as *Salamandra* and *Ambystoma opacum,* and by the fact that all the forms now undergoing lung reduction, those which have partially aborted lungs, are in quite a degree aquatic and associated with running water.

Boulenger suggests also in the same paper (p. 87) that the Plethodontidae, which all lack lungs, are "small or very small" forms and thus do not need the lungs, which, presumably, larger forms would find necessary. To this it is only necessary to say that while the Plethodontidae includes the smallest of all salamanders, *Oedipus townsendi* of Mexico, fully adult at a total length of 40 mm, it also includes numerous forms of quite respectable dimensions, the largest species, *Oedipus bellii,* reaching 275 mm, while twenty-one species of the family reach a length of six inches or over. A good many of the forms, then, are larger than animals in other families which have well-developed lungs.

Boulenger suggested in 1917 (p. 802), alluding to lungless salamanders in general, "The greater part of the species in which the absence or regression of the lungs has been determined live in obscurity, or more or less shaded from the active light, a mode of life which tends to render the gaseous exchanges of respiration less active." This is doubtless entirely true, but it is a remark which holds good for all salamanders, both lunged and lungless. Certainly the species of *Ambystoma* and *Hynobius,* which are burrowing and secretive as every collector knows, live far more in obscurity and shaded from the active light than do the species of *Desmognathus*

and *Eurycea* which haunt the banks of our brooks, and yet the former groups have lungs, and the latter do not.

Noble, in 1925, has a lengthy criticism of the whole problem, in which it seems to me that he overemphasizes the respiratory feature, and underemphasizes the hydrostatic, and in consequence takes little stock in the factor of current. This may be partly because he considers frogs and salamanders together, although the relative importance of respiratory and hydrostatic functions of the lungs is quite different in the two groups.

There is no experimental proof possible one way or another. Noble notes certain exceptions to the rheotropic adaptation theory put forward by Lönnberg, Mrs. Wilder and myself, and goes on to propose one of his own, which is a modification of that of Boulenger (1917).

Let us take first his exceptions. *Ranodon sibiricus* lives almost entirely in the water of mountain streams, and yet has not lost or absorbed its lungs. Does this exception destroy the validity of our thesis? It certainly constitutes a perfectly valid objection to it, which I can only answer in part by suggesting that *Ranodon* is a recent immigrant into the mountain brook habitat. Thus the egg-laying habits are practically identical with those of the parent genus *Hynobius,* a pond-breeder, and very different from those of the brook Plethodontids and of the species of *Euproctus.* In this respect it evidences less adaptation to the habitat, and hence, perhaps, a more recent entry into it. Again, the larva of *Ranodon* has, at least in early life, a dorsal fin, which even *Dicamptodon* has discarded. This seems to indicate imperfect adaptation and hence recent entry. Noble lays stress on the feature of *Ranodon* being aquatic rather than a dweller on the border of the brook. Here the observations of Snitnikov seem not wholly convincing, for while he pictures a typical mountain brook habitat, he does say that they emerge "towards beginning of evening," and that they can be found "out of water" and even "sometimes

pretty far away among Juniper bushes." This is not a picture of a totally aquatic beast.

The second exception noted by Noble is *Ambystoma altamirani.* Here I can, from personal experience, support the observations of Gadow that they never leave the water. The animal has well-developed lungs and is a stumbling block in the path of the rheotropic theory. But both Gadow and I noticed that while the adults live only in the running streams the larvae may be found in still water, in fact, I found the larvae only in ponds. Furthermore, the larvae have dorsal fins and thus are not at all of a stream type, for no thoroughgoing stream larvae, whether of frogs or of salamanders, have dorsal fins. Thus it would seem another case of imperfect adaptation and recent entry. This is very well borne out by the range of *A. altamirani,* for, I was told, when I was in Mexico, that the animal lived only in streams flowing over the Pedregal, a lava flow so recent that human remains are found beneath it.

I do not believe that these two cases, which seem to me recent invaders of the habitat, really demolish the theory that lungs are lost as rheotropic adaptation.

A third exception, *Salamandrina,* lacks lungs, and according to Noble, is not a brook beast. Here both he and I must fall back upon the observations of others as to the habits. It may be added that the animal shows, in its eggs and its larvae, none of the characteristics of mountain brook forms; but the various adaptations necessary to an animal taking up this habitat are not necessarily taken on in any regular order. Larvae of *Ranodon* have, in later life, an aborted dorsal fin, although the adult shows no modifications. Perhaps in *Salamandrina* the adult is more modified than the larva. What is its habitat? Here the only source of information is the copious European literature on this animal. The various observers agree that it lives

> in the closest proximity to . . . small rivulets . . . which run in gorges from the mountains down to the sea . . . which, like all mountain brooks

turn into raging torrents after thundershowers, but later dry up almost entirely, and only here and there maintain a few pools in their beds . . . the salamanders hide under stones or live in damp slime . . . both in spring and fall on rainy days they show themselves outside their hiding places, but during summer only after thundershowers . . . in March they go into the water to lay their eggs . . . very many such eggs are swept away by the water and buried in the sea . . . they are especially common in watered ravines . . . they absolutely avoid still water.

And this is the animal which Noble says (1925, p. 390) "may have arisen directly [from *Triturus* or *Notopthalmus*] without ever having occupied the mountain-brook habitat"! I myself should view the derivation from *Triturus* as highly probable, the animal differing from *Triturus* only in having four toes, in lacking lungs and in habitat. The chief difference in habitat, and indeed the only difference, is the presence of a current factor, to which the animals must all be subjected at one time or another in the course of their lives. It seems more reasonable to suppose that this is correlated with lack of lungs, than to follow Noble in calmly denying the existence of the habitat, and offering no alternative explanation for the absence of lungs in *Salamandrina.*

The only modification noticeable in *Salamandrina* is the lunglessness of the adult. In *Dicamptodon* the only modification is the lack of dorsal fin in the larva. (I can not regard the reduction in length of gills as necessarily significant. They are reduced in *Batrachuperus,* which has a dorsal fin, and is taken from ponds; they are not reduced in *Eurycea* or in *Gyrinophilus,* which certainly live in current.) *Dicamptodon* is considered a mountain-brook animal by Noble, and the fact that its lungs are not reduced is to him evidence against the rheotropic theory. While there may well be incomplete adaptation here again, the most recent account of the life history of *Dicamptodon* would indicate that the animal comes under the influence of current only slightly. Storer (1925) describes the eggs, laid in "Costen Lake" and differing essentially in form and situation not at all from those of the eastern pond-breeding *Ambystoma maculatum.* The

larvae may be found in the same pond, but may also be found in "creeks" where there is presumably current. The adult is notoriously terrestrial, an inhabitant of damp forests. Thus *Dicamptodon* is only occasionally a brook beast, and has only a modicum of the complete series of brook adaptations, which, in the thoroughgoing brook forms extend to the eggs, the larvae and the adults. It does not seem to me to make a valid objection to the rheotropic explanation of lunglessness.

To turn from the exceptions to the normal, completely adapted, brook type, the primitive Plethodontidae or the species of *Euproctus,* Noble denies the efficacy of the current factor, saying that these forms "live primarily along the margins of the brook" and "come during adult life under the influence of this current factor only at such intervals as when seeking to avoid their enemies, or, in some cases, when laying their eggs," and so he tends to think that "Boulenger (1917, p. 802) has pointed out the more important factor" in the phrase quoted previously, while he himself also tends to stress (1925, p. 391) "the greater oxygen supply in cold and in running water."

Boulenger's "more important factor" has been shown above to be inefficacious in many cases where it is more obviously a feature of the environment than it is in the surroundings of the normal lungless salamander. It remains to consider "the greater oxygen supply in cold and in running water," which, at first sight, would seem to be removed from the argument by Noble's contention that the beasts enter the water only at intervals, or upon special occasions. None the less the point has interest, and I have been at some pains to investigate the facts of the matter. Noble quotes the Smithsonian Tables of Physical Constants to show that the maximum gaseous content of water increases directly with a fall in water temperature, which is an unquestioned phenomenon, but one which leads him to the somewhat questionable conclusion that "cold, highly aerated water, contains, therefore, nearly half again as much oxygen as pond water."

This last sentence demands examination. At first sight it would seem to read, "Highly aerated water contains therefore half again as much oxygen as water which I consider not so highly aerated." The point of course is not whether cold water can contain more oxygen than warm, but how much oxygen actually is in brook water and how much in pond water, for pond water is not necessarily warmer than running water as every farm lad who can swim knows. If the animals do not normally enter the water, as Noble claims, the aeration of that medium is immaterial, for it is difficult to conceive of the air along a brook bank being more highly aerated than the air anywhere else.

The oxygen content of Wisconsin lakes has been measured by Birge (1908, p. 1275) and he finds it highly variable, but seldom below 6 cc per liter, and in some cases as much as 15 cc per liter. I had failed, despite considerable search, in finding any more reliable measurement of the oxygen-content of brook water than the frequent statement that it was "high," but a very recent abstract[3] gives the oxygen content of brook-trout waters in Michigan as from 1.7 to 6.3 cc per liter, and so the beau ideal of running streams has considerably less oxygen in its water than the less prepossessing pond. Creaser states that the oxygen content of the streams was "not directly correlated with the temperature of the water" and that the increased capacity of cold water to absorb oxygen "does not seem to keep the dissolved oxygen content of trout water above that of other waters. The relative absence of oxygen-consuming material and the relative amount of aeration are apparently far more influential than the temperature in determining the amount of dissolved oxygen present."

Thus if the oxygen content of the water is the important factor pond salamanders should be lungless and brook salamanders should have lungs. It might, indeed, be not implausible to reverse the entire argument and to

[3] Creaser, 1927, p. 171.

suggest that lunglessness might be a consequence of water which lacks oxygen, for in this way one could account for the reduction of lungs in the two frogs *Ascaphus* and *Batrachophrynus,* the former inhabiting the cold streams of the Olympic Mountains, and the latter the deep lakes of the Andes, where it lives along the bottom. Birge points out a sudden drop in the oxygen content of lake water just before the bottom is reached. Of course both of these localities are cold, but it is easy to point out many frogs which live in places as cold or colder, and which, none the less, have perfect lungs. Among salamanders *Hynobius keyserlingii,* dwelling north of the Arctic Circle at Verkoyansk, the North Pole of cold of the entire world, with perfectly good lungs, is evidence of the comparative inefficacy of this factor of temperature, while the lungless *Oedipus platydactylus,* which I have taken under a flat rock in an open field under the tropical sun of Jalapa, somewhat south of the Tropic of Cancer, is an example of the other extreme.

To revert, Shelford (1913, p. 99) says of the swift stream habitat that the three especial factors of this environment are necessity for rheotaxis, low temperature and high oxygen content. The last is apparently illusory, the second may be far surpassed elsewhere, and the first is left as the one peculiar condition of the brook habitat which may be correlated with the equally peculiar characteristic of lunglessness which seems to crop up in so many unrelated brook salamanders.

Dr. Noble published in 1927 some observations of habits of various Plethodont species in the Southern Appalachians, after six days spent in collecting some 325 specimens. It may seem unduly rash of me to take any exception to these observations, but I have spent more than eighty days collecting in that region, and my collections number more than 1,500 specimens, and it seems necessary to comment upon them in order to prevent (in the Elizabethan sense) misapprehension.

I found difficulty in discovering ecological differences between *Plethodon metcalfi* and *Plethodon glutinosus,* although I had found *glutinosus* from sea-level to 4,200 feet, and *metcalfi* from 3,000 to about 5,000 feet, an overlapping of 1,200 feet. Noble found *glutinosus* up to 5,000 feet, and *metcalfi* as low as 2,300 feet, and hence less segregation than I did.

In this region *glutinosus* was very common at 4,200 feet, at which point *metcalfi* abounded, and so I could see nothing distinguishing them ecologically. That *glutinosus* could stand regions of lower humidity than the Southern Blue Ridge was obvious, but it seemed to me to reach its maximum abundance there, while *metcalfi* also seemed to find its optimum there, but to be more narrowly limited.

Nevertheless Noble emphasizes the situation, remarking, "a gradual change in the moisture and oxygen requirements . . . it seems probable that one or both of these factors played an important part in the evolution of the species of *Plethodon.*" Since all Plethodons are completely terrestrial it is hard to see where any "gradual change in the . . . oxygen" occurs, unless the animals are sensitive to the slight change in the oxygen content of the air in passing from sea-level to 5,000 feet. *Glutinosus* is found in such abundance at 4,200 feet, practically in the middle of the 2,700-foot altitudinal range of *metcalfi,* that it is difficult for me to conceive of any environmental factor playing a very great part in the divergence of these species. Their size differences are at least much more noticeable than their ecological differences.

In *Plethodon,* Noble has found less difference than I did in habitat, and has emphasized it more. In *Desmognathus,* conversely, he has found more habitat difference than I did and has minimized it.

He (p. 2) distinguishes between "the smaller rocky streams or cascades of the mountain sides" and "the muddy and moss-grown trickles of both mountain and

valley." In a note he says "muddy" refers "to the character of the stream bed, not to the water." "In the rocky streams or trickles *Desmognathus quadra-maculatus* is ubiquitous, while in the leafy trickles *D. phoca* is the dominant salamander." "I never found an adult *quadra-maculatus* in a muddy trickle, or an adult *phoca* in a rocky stream, but the half-grown individuals occur in both types of habitats." Whereupon he proceeds to disagree with a general statement of mine (1926, p. 17) to the effect that *D. phoca* "instead of being, like *quadra-maculatus,* an animal of streams, . . . is a creature of the banks of smaller brooks." I fail somewhat to see the difference between his statement and mine, especially as in the more detailed accounts of the habits I give examples of considerable wandering, not only by half-grown animals, but by adults. From my own experience, the first adult, a very large one, of *quadra-maculatus* which I caught, was taken in a decidedly muddy brook near Brevard, while I never saw *phoca* (including the largest males and females on record) more common than in a ravine near Midway Mills, Va., where the brook ran over a rock bottom among numerous slabs of shale. Pope, who worked in the same localities as Noble at Flat Rock, contradicts him regarding the "muddy" character of the stream bed thus (1924, p. 7–8) "*phoca* was found in every rocky stream hunted. Unlike *quadramaculatus,* it does not frequent deeps and rapids of the larger, swifter streams." Of the bed of a brook where *phoca* eggs and adults were found "the bed of the brook . . . is made up of sand, gravel and small stones." Of a larger stream elsewhere, Boone Fork, Pope says (p. 14): "The author can not recall seeing more than one *phoca* in Boone Fork."

In general the amount of water, and the fact that *phoca* lays its eggs out of water, while *quadra-maculatus* lays its eggs under water, and the longer larval life of the latter, are the factors which led to the general statement which I made, and have quoted above, and should

repeat. The wandering away from the breeding site is not so great in these salamanders as to falsify a *general* identification of the breeding site with the habitat, an identification which might well be incorrect in many frogs, or even in other salamanders.

Of *Pseudotriton* Noble says (p. 3): "Some species, such as *Pseudotriton montanus,* may be so constituted as rarely to move far from their breeding streams" and (p. 5) "nor does *Pseudotriton ruber* compete with *P. montanus,* although outside of the breeding season the former may wander considerably," and (p. 24, under Conclusions) "competition between some closely related species . . . is avoided . . . (as *Pseudotriton*) by preferences for different types of streams, at least during the breeding season."

The above is entirely gratuitous assumption. There are no other references to or observations on *Pseudotriton* in the paper under discussion, nor has Noble published anything elsewhere concerning its habits, nor have any recent additions been made to the knowledge of them. As a matter of fact, *montanus* also is known to wander occasionally quite far from water, and the fact that such observations are few (two) is easily accounted for by the paucity of observations on this form. The egg-laying habits of the two are known to be fairly different, and their different bodily shapes seem correlated with a general preference on the part of *montanus* for more muddy localities, not necessarily only during the breeding season. Both have, however, been taken at the same spring; and in regions where one is common the other is rare, which would seem to indicate that there is some competition.

Finally, with regard to *Batrachoseps,* a worm-like form with which neither Noble nor I are acquainted in nature, he says:

> It is easy to imagine that every phylogenetic change in the organization of an animal is adaptive. . . . Dunn (1926, p. 26) says of *Batrachoseps:* "Ecologically this elongate type is a further advance [over *Plethodon*] in

terrestrial adaptation and bespeaks a burrowing mode of life.'' But Storer (1925, p. 97) . . . assures us that ''there is no evidence that *Batrachoseps* actually burrows in the ground.'' . . . Whether *Batrachoseps* follows crannies to greater depths than *Plethodon* is an uncertain question. It is far simpler to label the elongate body of *Batrachoseps* . . . as specializations until they are proved to be adaptations in the usual sense of the word.

Again I fail to see Noble's point. Any one who has ever kept salamanders in terraria knows full well that even such non-elongate forms as *Desmognathus* and *Plethodon* make their own burrows and do not merely ''follow crannies.'' Why, then, is it so wrong to suggest the same capability in *Batrachoseps*? I have actually seen the similarly worm-shaped ''Oedipinas'' burrowing like earthworms, and many have been taken during ditch-digging operations, along with the equally worm-like and burrowing Coecilians. *Batrachoseps* disappears underground during the dry summer of California. There may be no actual evidence that it makes its own burrows, but the correlation of a worm-like form and a worm-like habitat seems to me an adaptation in the usual sense of the word, *i.e.*, an obvious physical peculiarity found in a peculiar habitat to which it seems fitted. The body shape of *Batrachoseps* bears definite relations to the life it leads, and it is far simpler to call such relations adaptations than, by an assumption of ignorance, to call them merely specializations. If the correlation of form and habit is not adaptation ''in the usual sense of the word,'' by all means let us have a new definition.

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# DEVELOPMENT OF TEMPERATURE CONTROL IN NESTLING HOUSE WRENS[1]

S. CHARLES KENDEIGH AND S. PRENTISS BALDWIN

## I. Introduction

The body temperatures of birds are very variable. This is true not only with young birds before they have become covered with feathers, but also of mature adults. Differences in the body temperature of the adult of as much as eight degrees may be normally expected to occur between various hours of the day and night. Indeed, differences of four or five degrees often occur within a few minutes.

Frequently in the literature of avian physiology and life history, statements are to be found to the effect that the body temperatures of nestling birds are extremely variable and similar to those of cold-blooded animals. In only a very few instances, however, has supporting evidence been given. Pembrey's work (1894, '95) has been the most convincing in this regard, although it is concerned principally with the carbon dioxide discharge of young animals rather than with their temperatures.

The purpose of this paper is to describe and discuss the extent of the temperature variation in young house wrens (*Troglodytes aëdon aëdon*) and to show how during the nestling period the temperature of the young bird passes from a condition of extreme variableness to that of comparatively lesser variability found in the adult. In other words, it will be the tracing of the development of temperature control in nestling house wrens.

## II. Instruments Used

Several instruments of different kinds were used in this study. Mercury thermometers and thermocouples

[1] Contribution No. 14 from the Baldwin Bird Research Laboratory, Gates Mills, Ohio.

were both used. However, as the work progressed, more and more reliance was placed upon the thermocouples, as it was found that the results obtained from their use was much more extensive, detailed and reliable than those obtained with thermometers.

All the mercury thermometers used were especially adapted for this study and made particularly for our purpose. These were fashioned after the ordinary clinical thermometer used commonly by physicians. They were self-registering and so necessitated shaking down between two consecutive readings. They differed from the clinical thermometer in registering temperatures from 90° to 115° instead of only to 110° F. The frequent obtaining of temperatures above this latter mark made this adaptation necessary. One make of these thermometers was of about the same shape and size as the medical thermometer, but with a bulb of smaller diameter. This kind was used primarily with adult birds. For young birds, thermometers of smaller diameter and with bulbs which were narrower and longer were used. This made the taking of temperatures of one- and two-day-old birds much more certain and easy, with less danger of harming the bird. A third kind of thermometer was much the same as the last described, but registered between 65° and 90° only.

After experimenting with readings down the throat, through the anal opening, under the wing and on the belly, it was found that the most accurate method was to thrust the thermometer down the throat of the bird until it had penetrated well into the body cavity, which meant usually that the bulb was down the gullet as far as the proventriculus. It was then left several seconds until the mercury ceased to rise, when it was removed and read.

All the thermometers used were certified by the manufacturers to be accurate to within one tenth of a degree Fahrenheit. Comparing readings of one thermometer with another showed that this accuracy could be depended

upon. All readings, both with mercury thermometers and thermocouples, were taken in the Fahrenheit scale.

Thermocouples were made in two ways so that they could be used for different purposes. Discussion of the principle of thermoelectricity together with a use of thermocouples in life history studies of birds has been made in a previous paper (1927) and needs no further mention here, except to say that it is a means of measuring the temperature at the warm end of a closed electric circuit by the amount of electric potential produced. This closed circuit is a thermocouple, the warm end of which is subjected to the temperature desired to be measured.

The thermocouple ends may be joined in such a way that a continuous wire thread is made and this may be stretched across the nest cavity. When the adult bird or nestling sits on this wire in the nest the surface temperature of the bird is obtained. Although this does not represent the body temperature of the bird, nevertheless there is a relation between the surface temperature and that of the body so that the data obtained have considerable value.

The other way in which the thermocouple was used was to twist the two ends of the wire together at the warm junction so that a thermocouple thermometer was formed. In making these, care was taken to use well-insulated wire and to allow the two metals to come into direct contact at only the very tips so that only at this point the temperature would be measured. In order to make the insulation back of the functioning tip doubly secure it was well coated with collodion so that when this hardened a smooth, firm, water-tight covering was formed. These thermometers were tested in various ways and found to function very satisfactorily. The tip of a thermometer was thrust down the bird's throat as with the ordinary mercury thermometer and equally as far. The thermocouple thermometer had the great advantage that it did not need to be removed after each reading but could be

left in the bird as long as desired, and several readings per minute could easily be made without touching the bird at all.

Two different instruments were used in measuring the potential induced by the temperature at the warm junction of the thermocouple. One of these instruments was a recording potentiometer so that continuous records plotted against time were obtained day and night on a ribbon of paper. Although this recording instrument has certain desirable features and gave certain data of great interest, its accuracy could not be depended on to a greater extent than about one degree plus or minus.

The instrument that was used the most and gave the most accurate data of any was a portable indicator potentiometer. The principle of its functioning is practically the same as with the recording instrument above, but instead of giving a spontaneous record, it must be balanced and read each time. Under favorable conditions about three readings could be taken per minute. This instrument is guaranteed by the designers to be accurate to within one half of one per cent. of its range, which in this case was four tenths of a degree. However, a new and more accurate galvanometer of a different type was introduced into the system so that after repeated tests against certified mercury thermometers a dependable accuracy of one tenth of a degree was assured.

One factor must be taken into account in getting bird temperatures. Thrusting a cold thermometer down the bird's throat lowers the body temperature a very appreciable amount, particularly if it is a small bird. An idea as to the amount of this lowering was obtained from some twelve experiments on English sparrow (*Passer domesticus*) juvenals and house wren nestlings. The body temperature was first read by means of a thermocouple thrust up into the body cavity, through the rectal opening. The mercury thermometer was then thrust down the gullet of the bird and allowed to remain a few seconds until its registering was completed. Meanwhile the drop in

body temperature was measured by the thermocouple, which was kept thrust through the rectum. Both instruments were then withdrawn. From this it was ascertained that a cold thermometer is very likely to lower the body temperature of the birds from seven tenths to over one degree Fahrenheit. However, since the rapidity with which the mercury thermometers register is very great and since the greater part of the heat absorbed by the thermometer is apparently by the glass above the bulb, the readings from the thermometer are usually only .2°–.8° lower than the original thermocouple reading of the body temperature. The warmer the thermometer is before thrusting it into the bird, the less will be the drop which it will produce. Using the same process it was found that thrusting a thermocouple down a young bird's throat caused a lowering of the body temperature only .1 degree to .2 degree. This drop with the insertion of the thermocouple is largely done away with when it is allowed to stay in the bird for a few seconds. For this reason it is thought that no correction is necessary with the readings of the body temperature obtained with the use of thermocouples. With mercury thermometers a correction is also impracticable, since the amount of error varies considerably under different conditions, but readings a few tenths of a degree too low may be regularly expected.

Before proceeding to the discussion of young bird temperatures, it is perhaps fitting to say that over sixty young birds, nearly all of them house wrens, were used in the experiments to be described. Approximately 3,300 readings were obtained on these birds during the last two summers. It will be noted that in nearly all instances these records are for live birds and were not obtained from birds recently killed.

## III. Experiments under Controlled Conditions

In order to obtain information on the extent of variation in the body temperature of nestling wrens from day

to day during the developing period, a set of experiments under controlled conditions was devised. The young birds were taken from the nest and carried to the experimental laboratory where they were subjected alternately to air temperatures ranging from 100°–104° to 66°–73° Fahrenheit. These temperatures were selected because they were the most convenient to use and because they approximated brooding and air temperatures in the nest.

These experiments were carried on in a basement room. As a consequence the air temperature was very uniform so that during the course of the experiments it varied only about seven degrees from one fortnight to the next. The average temperature was slightly less than 70°, and it was to this temperature that the birds were subjected. The higher temperatures were obtained and maintained within a four-degree variation through the use of an incubator. The bird under study was merely placed in this incubator and the door closed. The small amount of variation in the room and incubator temperatures was not great enough to be of any significance in modifying the condition of the experiments.

Readings of the body temperature of the young birds were taken with thermocouple thermometers and the indicator potentiometer. As the thermocouple wire was short and thin it was possible to run it around the edge of the incubator door when the bird was inside and the door closed. When moving the bird from the incubator to a small open box in the room to subject it to lower temperatures or *vice versa* to replace it in the incubator from this box, the act was done quickly in a few seconds without even removing the thermocouple from the bird's throat. The air temperatures of room and incubator were read with thermocouple thermometers placed between one and two inches away from the bird.

When the young bird was first brought into the room, the thermocouple was inserted down its throat and the bird was placed in the incubator for a few minutes until its body temperature had risen to a hundred or more

degrees. It was then removed and replaced in the room at about 70° temperature. As the bird's body temperature dropped, frequent readings with the potentiometer were taken. The bird was allowed to remain in the room until the drop in its body temperature came to a stop and an equilibrium was reached. The bird was then replaced in the incubator and the rapidity with which its body responded to the air temperature there of about 102° was recorded. The bird was left in the incubator until it appeared that its temperature would rise no more and that the new equilibrium between internal and external heat was reached. Each such experiment required between two and four hours to complete and these were carried out almost entirely in the mornings. The young bird under experiment, of course, received no food during this period.

A different bird was selected to represent each day in the nestling period, and each day's record was verified from one to three or more times with other birds so that a large number of nestlings were used. The work extended over the summer and so several different wren broods were studied. The graphs and tables included in this paper are not, however, averages, but are single records of individual birds which appeared to respond to the temperature variations in the most typical way.

The experimental room was well adapted to keep such factors as light, humidity and circulation uniform and the same inside the incubator as outside. The room was originally intended to serve as a dark room for photographic purposes. Hence the light factor was very much under control. Inside the incubator, light was absent. In order to minimize any effect of bringing the bird from a very dark place to a light one, the room was kept dark with only enough illumination to permit reading the instrument. Occasionally a ruby electric light bulb was used. The relative humidity inside and outside the incubator was measured at the beginning and end of each experiment by stationary hydrometers. Care was taken to

TABLE 1

BODY TEMPERATURES OF NESTLING HOUSE WRENS UNDER CONTROLLED CONDITIONS

| Age | | Temperature of young in room, room temperature in parentheses | Difference between bird and room temperature | Average temperature of bird in incubator, incubator temperature in parentheses | Average difference between bird and incubator temperatures |
|---|---|---|---|---|---|
| Days | Hours | | | | |
| 1st | 1 | 71.5° F. (71.1°) | + 0.4° F. | 102.9° F. (102.2°) | + 0.7° F. |
| 2nd | 26 | 69.5 (68.9) | 0.6 | 102.5 (102.0) | 0.5 |
| 3rd | 42 | 71.5 (70.7) | 0.8 | 104.3 (102.1) | 2.2 |
| 4th | 74 | 69.9 (69.0) | 0.9 | 105.1 (102.9) | 2.2 |
| 5th | 97 | 76.2– 76.4 (72.7) | 3.5– 3.7 | 105.9 (102.9) | 3.0 |
| 6th | 120 | 77.9– 78.2 (71.7) | 6.2– 6.5 | 106.2 (102.5) | 3.7 |
| 7th | 145 | 81.3– 82.8 (71.8) | 9.5–11.0 | 106.1 (103.0) | 3.1 |
| 8th | 171 | 78.3– 82.6 (69.6) | 8.7–13.0 | ..... ..... | ..... |
| 9th | 193 | 83.7– 96.5 (69.6) | 14.1–26.9 | ..... ..... | ..... |
| 10th | 213 | 90.8–102.3 (71.0) | 19.8–31.3 | 106.0 (103.0) | 3.0 |
| 11th | 240 | 99.5 (67.7) | 31.8 | 107.8 (102.5) | 5.3 |
| 12th | 264 | 101.5 (68.0) | 33.5 | 108.5 (102.5) | 6.0 |
| 13th | 288 | 104.6 (67.5) | 37.1 | 109.4 (102.3) | 7.1 |
| 14th | 315 | 105.3 (69.9) | 35.4 | 108.8 (102.0) | 6.8 |
| 15th | 336 | 107.8 (67.9) | 39.9 | 111.6 (102.6) | 9.0 |
| Adult male | | 107.5 (68.0) | 39.5 | 118.2 (102.7) | 15.5 |

prevent a difference greater than ten per cent. between the two positions and this was successfully done on all except two occasions when it was a few per cent. more. The average humidity during the experiments for inside the incubator was 77.2 per cent., while that for the room outside was 80.9 per cent. The range from day to day was of small extent. The amount of circulation of air inside the incubator was sufficiently great as tested by the confinement there of birds for several hours at a stretch. Occasionally birds were kept thus for over twenty-four hours with no ill effects. In the room itself there were no drafts perceptible, as practically all the cracks and openings had been closed to shut out the light. Hence, it is certain that with these other factors constant, the temperature variable was the only one affecting the reactions of the birds.

Little difficulty was experienced in keeping the thermocouple down the throat of the very young bird. With the older birds, use was made of a small, large-meshed, loosely fitting sac into which the bird was placed and to which the thermocouple was occasionally fastened. Movements of the wings and legs were not prevented in either the young birds or the older ones. This amount of movement was permitted, as it was thought that activity might be a factor in the temperature control.

A careful study of the graphs and table (Table I) should be sufficient to obtain an idea of the results of these experiments and so extensive text explanation is unnecessary. It is at once obvious that the amount of variation in the body temperatures of the first- and second-day birds is extreme, but that as the birds become older the extent of this variation decreases until on the last day it is only slight.

Considering first the drop in body temperature when the bird is subjected suddenly to a change from an air temperature of approximately 102° to one of 70°, a few facts may be called to attention. In practically all instances, the birds responded to the change immediately.

In the youngest bird it was the most rapid. For instance, in the case of the one-hour-old bird (Fig. 1) its body tem-

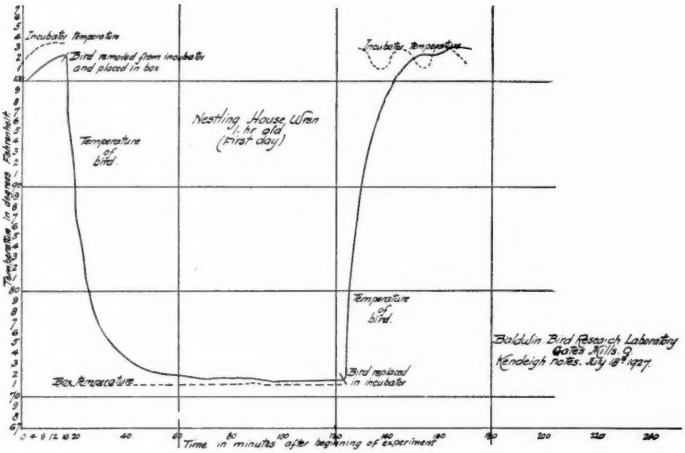
Incubator temperature
Bird removed from incubator and placed in box
Nestling House Wren 1 hr old (First day)
Temperature of bird
Incubator temperature
Temperature of bird
Bird replaced in incubator
Box temperature
Baldwin Bird Research Laboratory Gates Mills, O. Kendeigh notes. July 18th 1927.
Time in minutes after beginning of experiment

FIG. 1

perature dropped from 100° to 80° in eight minutes. In an eight-day (171 hours) bird (Fig. 3) this 20° drop extended over a full hour and hence was considerably slower. There is a gradual slowing up of the rate of this drop from day to day.

The response of the one-hour bird to a change from 70° to 102° in the air temperature was not so rapid, although it began immediately. It required nineteen minutes for the bird to rise from 80° to 100°. There is apparent a slight slowing up of this response to high temperatures in the older bird, but it is so small as to be questionable and not nearly so evident as the slowing up of the rate in the temperature fall.

The temperature of the one-hour bird dropped until it was only 0.4° above that of the box. In no case did the body temperature of any of the live birds actually reach that of the box; always it was higher, even though during the first four days it was only a few tenths of a degree. That this was not due to not permitting the birds to re-

main at the low temperature a sufficiently long time is shown by one experiment where a nestling wren something more than three days old was left at a box temperature of 65°–66° for thirteen hours and fifty minutes. An equilibrium was reached at an average of 1.5° above that of the box and this was maintained with very little variation. Only once was its body temperature recorded lower than one degree above that of the air (0.6°) and only once was it recorded as high as 1.9° above. The temperature of this bird was somewhat above this average during the first part of the period and slightly below during the latter part.

From day to day the extent to which the temperature of the young bird dropped decreased (Table I). During the first four days (seventy-four hours) this decrease was only a few tenths of a degree. On the fifth day, and practically every day thereafter, it was decidedly more. Beginning with the fifth day also there is perceptible a slight rise in body temperature after it has first dropped to its minimum point (Figs. 2, 3, 4). On the ninth and tenth days this spontaneous rise of body temperature without addition of external heat amounted to over ten

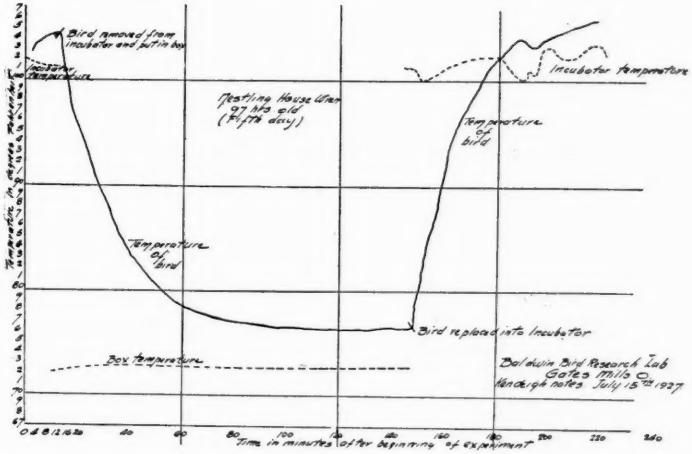
Bird removed from incubator and put in box
Incubator temperature
Nestling House Wren 97 hrs old (Fifth day)
Temperature of bird
Incubator temperature
Temperature of bird
Bird replaced into incubator
Box temperature
Baldwin Bird Research Lab Gates Mills O. Hendrigh notes July 15 to 1927
Time in minutes after beginning of experiment

FIG. 2

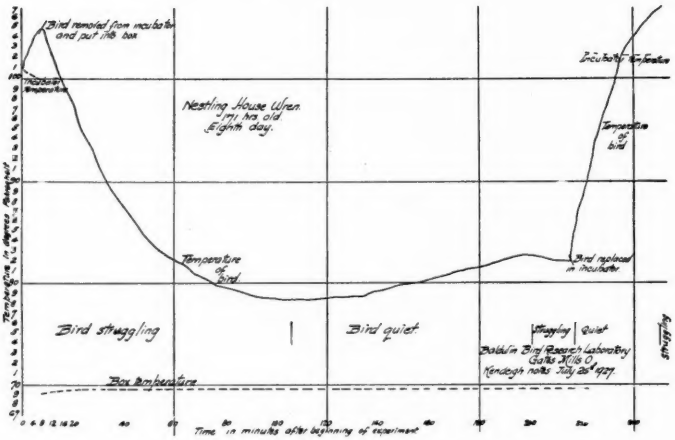
Bird removed from incubator and put into box
Incubator temperature
Nestling House Wren 7m hrs old Eighth day.
Temperature of bird
Bird replaced in incubator
Bird struggling
Bird quiet
Box temperature
Baldwin Bird Research Laboratory Gates Mills O. Kendeigh notes July 26th 1927
Time in minutes after beginning of experiment

FIG. 3

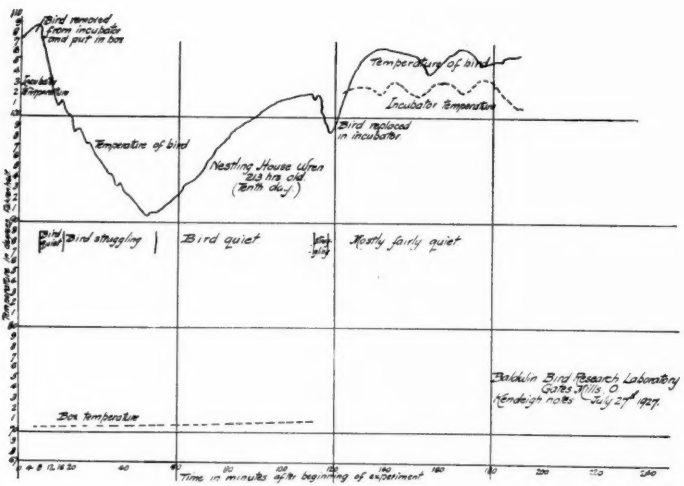
Bird removed from incubator and put in box
Temperature of bird
Incubator temperature
Bird replaced in incubator
Temperature of bird
Nestling House Wren 213 hrs old (8th day)
Bird struggling
Bird quiet
Mostly fairly quiet
Baldwin Bird Research Laboratory Gates Mills O. Kendeigh notes July 27th 1927
Box temperature
Time in minutes after beginning of experiment

FIG. 4

degrees. From the eleventh day on (Fig. 5), the control of body temperature was much more efficient and did not drop so suddenly nor so much as before. During the last day or two the transferring of the bird to an air temperature of 70° had very little, if any, effect.

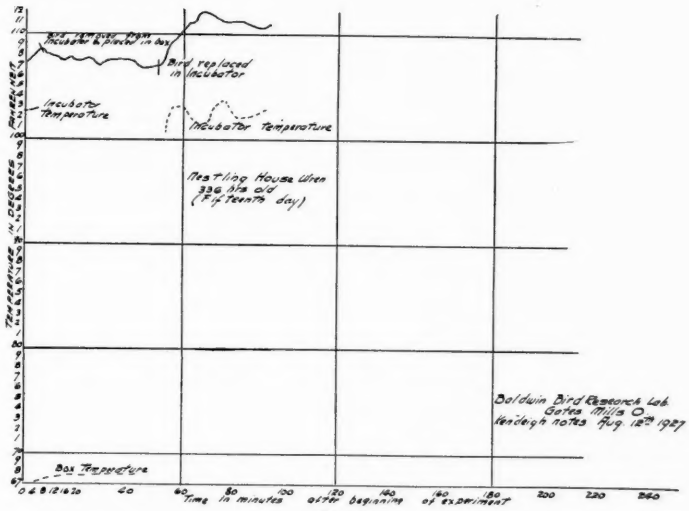
Bird removed from incubator & placed in box
Bird replaced in incubator
Incubator Temperature
Incubator Temperature
Nestling House Wren 336 hrs old (Fifteenth day)
Baldwin Bird Research Lab. Gates Mills O. Verdeigh notes Aug 12th 1927
Box Temperature
Time in minutes after beginning of experiment

FIG. 5

The development of the control against intense air heat is much less marked than against cold. In fact, each day during the nestling period, the body temperatures of the young birds rose higher and higher above that of the incubator. This rise was gradual at first, but during the latter days in the nest it was slightly faster. Apparently the development of a temperature control in wrens against intense heat is very slight, if any. This was strikingly shown in the case of an adult male wren which was transferred from the room temperature of 68° which had had no effect upon it to the incubator temperature of 102°. Within twenty minutes its body temperature rose from 108° to 118.2° and undoubtedly would have gone higher had it not been removed.

Plotting the number of degrees temperature which the nestlings were able to attain above that of the room from day to day gives a distinctly sigmoid curve (Fig. 6). This curve indicates the rate at which a resistance against cold is developed by the young birds. In many respects this curve is comparable to the growth curves of Robertson

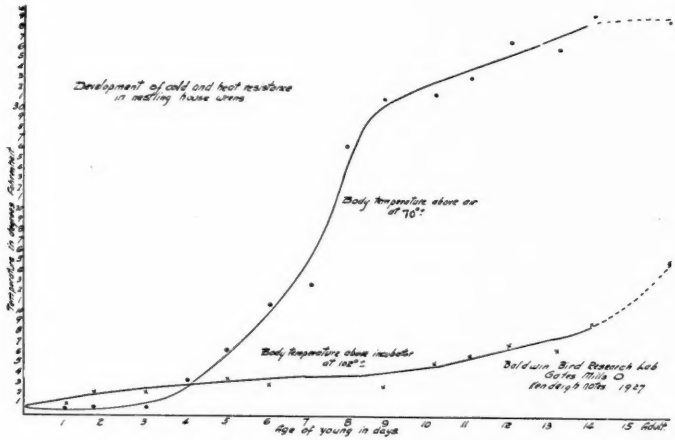
Development of cold and heat resistance in nestling house wrens
Body temperature above air at 70°F.
Body temperature above incubator at 105°F.
Baldwin Bird Research Lab Gates Mills O Kendeigh Nov 1927
Age of young in days
15 Adult

FIG. 6

(1908) and others. One unique feature of this particular curve is that it is for the development of a function rather than a structure, as has been the case with the majority of growth studies hitherto where the S-shaped curve has been obtained. This function is, however, dependent upon the development of structural characters. An analyzation was made of the factors entering into the make-up of this curve and these were found to be several. These may be considered separately.

The weight of nestling wrens increases rapidly during the first week and attains about five sixths the weight of the adult bird by the end of ten days. Growth in body size, exclusive of feathers, corresponds closely and extends over a similar period. This increase in size and weight was thought to have considerable significance in the decrease in rate of temperature response as the nestlings became older. Certainly masses of great size respond to temperature variations more slowly than do masses of small extent due to the smaller proportion of exposed surface to the body of the mass. Accordingly a set of experiments were carried out with birds of different sizes and weights. Six birds in all were used

ranging in age from birds just out of the shell to those seven or eight days old, and ranging in weight from 1 g. 22 mg. to 6 g. 662 mg. Feather development outside the body was not sufficient to be a factor in these experiments, and since the birds were dead no internal organs or metabolism could modify the results. From this it was seen that increase in mass did produce a very perceptible slowing up of the rate at which the temperature of the body dropped from incubator to box temperature. In the largest bodies the drop from 100° down to 80° was over three times slower than in the smallest bodies. The response to heat from the outside was also slower.

The drop in body temperature of a dead bird was much faster than of a live one of the same weight and size. Two birds approximately three and five days old and weighing 2 g. 771 mg. and 6 g. 200 mg., respectively, were used in determining this. While alive and active, the birds were placed at incubator and room temperatures and the rate at which their body temperatures dropped, and later when returned to the incubator rose again, was determined. The birds were then killed with electric shocks and the process of subjecting them to room and incubator temperatures repeated immediately. The response of the dead bodies to the cold temperatures was about one and a half times faster than when the birds were alive. The response of the dead bodies to the high temperatures was only a trifle faster. As any special temperature-regulating apparatus within the bird is not effective at this stage of their development, the above data would suggest that the metabolism of the bird and consequent production of heat is of aid in retarding rapid lowering of body temperatures.

As has already been stated, no live bird ever actually reached room temperature but always came to an equilibrium at least a few tenths of a degree above. However, all the dead birds did reach the room temperature, either actually or to within a tenth of a degree. From this it would appear that the number of degrees or tenths of a

degree which a live bird maintains its body temperature above that of the air represents the extent of the equilibrium between heat production within the bird and heat dissipation. Any increase in the number of these degrees would mean either that heat production was greater or the amount of heat loss had been lessened or that both factors had been modified. Our experiments indicate that the second of these alternatives is the more important, although doubtlessly with increased mass of body as the birds become older the actual amount of heat produced is greater. Perhaps, also, the bird may develop some ability to regulate the amount of heat produced at different degrees of external temperature, but this was not determined.

According to Wetmore (1921), Pycraft (1910) and others and from work of our own, the use of the air sacs together with the respiration as a means of temperature regulation in adult birds seems very likely. If so, is there any evidence as to when they begin to function in nestling birds?

After dropping to a temperature 3.5° above that of the room the body temperature of a fifth-day bird (ninety-seven hours) rose two tenths of a degree (Table I). This alone would not be of much import were it not that the least difference between bird and room temperatures was 2.6° above what it had been the day before and this represents an increase considerably greater than what had taken place during the preceding days. This can not be explained by any sudden increase in mass or heat production nor by the appearance of feathers. Feathers as a thermal covering can have little effect before about the eighth day. On the sixth day the least difference between bird and room temperatures shows another distinct rise over the preceding day, while the greatest difference is 0.3° above this. This 0.3° represents a spontaneous rise in the temperature of the bird without any similar increase in the air temperature. This spontaneous rise in temperature is clearly shown in Figs.

3 and 4. From the seventh to tenth days, inclusive, the increase in the number of degrees which the birds raise their temperatures above that of the room is extreme. Undoubtedly a part of the increase in the least differences between room and body temperatures may now be attributed to the breaking open of the pin feathers to form a protective covering against heat loss. However, the putting on of feathers does not explain the fact that after the body temperature of the bird drops to these low points it later rises again so that on the ninth and tenth days it nearly attains the original point from which it dropped. This we believe represents the coming into effectiveness of a definite apparatus within the body of the bird designed for the control of its temperature.

It will be noted from the graphs that when the young birds are actively stirring and moving about, their body temperatures drop rapidly but that when they are quiet they rise (Figs. 3, 4). While active, they probably make more heat than when quiet, but it is given off faster, due to a more rapid rate of respiration and possibly greater exposure of body surface. While quiet, they are apparently saving the greater proportion of the heat produced. From watching a large number of young birds behave in this manner it became quite evident that the rise and fall of temperature has some close connection with the amount of visible breathing.

Any evidence that saving of heat produced is largely affected through retention of the warmed air in the air sacs is only indirect at present. We have in mind certain anatomical studies which we believe will shed considerable light on this point in the future. Gross anatomical examination of young birds a few days old did not reveal the presence of air sacs. On two different occasions, however, we have found nestling wrens in a pathological state where the air sacs, particularly the abdominal air sacs, were greatly bloated. Since these birds were nine and ten days old, it means that the air sacs were becoming mature at that time. It is probable that they do not be-

come entirely effective until several days after the young leave the nest.

When the pin feathers begin to break open an insulating cloak becomes wrapped around the body which is of considerable significance in helping the bird maintain its body temperature within a fairly constant range of degrees. An English sparrow juvenal was subjected to incubator and room temperatures and all variations in its body temperature recorded. The bird was very persistent in maintaining its temperature about 106.7° in the room. The largest part of the feathers of the bird was then clipped off with scissors and the bird again subjected to incubator and room temperatures. In the room it was able to maintain its temperature around 104° for about half an hour, but later in the experiment it fell to 88.8° when work was stopped. The bird had some ability to maintain its body temperature without feathers but not for a very long time. The rise in the curve of temperature control during the last few days undoubtedly is in part due to the growth of this feather covering and consequent increased protection against heat loss.

The development of a feather covering for the naked skin may be of very distinct value in enabling the bird to keep its temperature from dropping, but it lessens its ability to withstand great heat. This is due to the insulation of the feathers, greatly reducing the amount of heat capable of being dissipated from the body surface. It is probable that with the very young birds the body temperature was only a few tenths of a degree above that of the incubator because the proportion of body surface to body volume was great and so excess heat was easily gotten rid of. As the bird grew and the proportion of surface to volume decreased, the bird's ability to withstand heat decreased and, of course, this was greatly added to when a feather covering was developed to cover up even this amount of dissipating surface. The development of an internal surface for controlled heat dissipation partly compensates for this loss of external sur-

face. This internal surface would be in the air sacs. That there were limits to its effectiveness is shown in the case of the adult wren mentioned. In natural life, birds probably avoid extreme heat far oftener than they resist it for any extended length of time.

One point of interest in these experiments is that not a single young bird died for reasons directly traceable to the exposure to low temperature to which they were subjected, even though this exposure in some cases was for several hours. On being replaced in the nest and brooded by the adult female they developed normally thereafter. We have in mind some further experiments to determine how low temperatures and how high temperatures young and old birds will withstand and for how long a time without showing ill effects.

### IV. Experiments under Natural Conditions

Variations in the body temperatures of birds of as much as thirty or more degrees under artificial conditions does not, of course, signify a similar degree of variation of the young in the nest, nor any variation in the nest at all, for that matter. Hence, considerable attention was paid to temperatures of the young birds in the nest under as natural conditions as it was possible to leave them.

One experiment was to determine and record the amount of variation in the body temperature of a young bird only a few hours old, during the periods of attentiveness and inattentiveness of the adult, that is, when the adult was brooding and when she was away. It was found possible to record the rise in the young bird's body temperature when the adult female was actually sitting on it and brooding.

When the nest-building activities first began at this particular box nest, which was located low down on a tree, a small movable building was drawn up close and the nest box transferred to this blind. The bird box was arranged for observational purposes by removing the wooden back and replacing this with a glass one. Then when the eggs

hatched a thermocouple thermometer like the ones used in the experiments above was inserted through the side of the box and nest and thrust down the throat of a young bird in such a way that it did not place the bird in an awkward position nor attract the attention of the adult when she came in to brood. Thread thermocouples were also run, one just above the young in order to obtain a record of the temperature applied to the bird by the brooding adult, and another underneath the young to get the temperature at the bottom of the nest. The ends of the thermocouple wires were then run back into the blind where readings were taken by means of the indicator potentiometer and observations were taken through the observation tube. The result is shown in graph (Fig. 7).

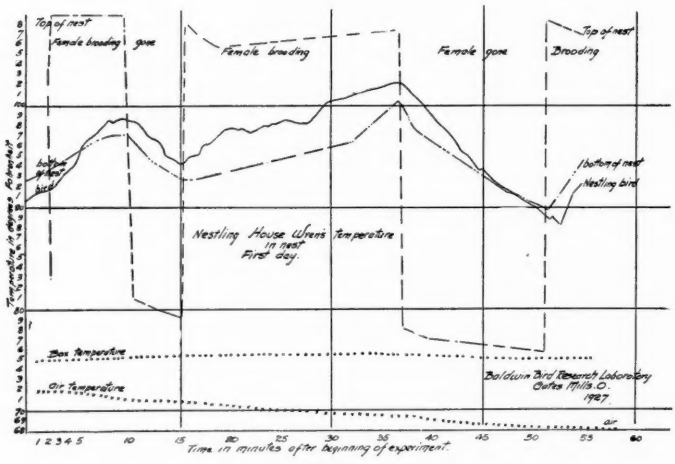


FIG. 7

It will be noted that the temperature of the young bird was between that of the top of the nest which, when the adult bird was brooding, was actually the belly temperature of the adult, and the bottom of the nest, although when the brooding adult was absent the temperature of the young bird did not drop below that of the bottom of the nest for several minutes, or if the period was short,

not at all. The rise and drop of several degrees in the temperature of the young bird when the adult was brooding and absent is so evident and indisputable as to need no further comment.

In order to get some further data on the amount of variation in the young birds' temperature while in the nest and the gradual increase in their body temperatures from day to day, use was made of the mercury thermometers. At the end of an attentive period when the adults had been brooding or feeding the young and again at the end of the inattentive period when they had been away the temperatures of one or two of the young were obtained by thrusting the thermometer down their throats without removing them from the nest box. It was necessary, however, to lift back the lid of the box in order to reach them and it was often necessary also to raise them partly out of the nest cavity. This disturbance may have had some influence in lowering their temperatures a slight amount. As soon as the adult appeared at the entrance hole at the end of a feeding or brooding period the box was approached and usually a reading could be obtained within thirty seconds after the adult had left the nest. At the return of the adult at the end of a period away she was usually allowed to alight on the perch in front of the entrance before being driven away and the temperature of the young taken. In this way the variation in the body temperatures of the young was obtained over natural intervals when they were alternately subjected to the attention and inattention of the adult bird. Data of this kind were obtained at two different nests, a first brood where both male and female were attentive and a second brood where the female alone was active. Readings were taken at the same time every morning during the nestling period when the temperature of the young was at about the average for the twenty-four-hour day. The young birds were not differentiated individually, but ordinarily each morning twice as many readings were taken as there were birds in the box, approximately half at the end of

the attentive period and half at the end of the inattentive period. Thus when there were seven young in the nest, fourteen records for the day were taken. Often the number obtained would run higher. It required in practically all cases from two to four hours each day to make the record since the alternating periods were long, and at intervals the adults were allowed to take care of their young without interference in order that the conditions at the nest and of the young could be kept as nearly natural as possible. The adult birds seldom paid any prolonged attention to the person doing the work with the young. When driven away from the box at their return with food or for brooding, they would ordinarily merely hop aside and wait until the temperature of the young was taken and then enter immediately. Thus the presence of a man continually at the nest did not modify their behavior to any great extent. It is believed that the temperature records are accurate to within one degree and that the natural behavior of the young in respect to temperature variations was determined very closely. Readings were also taken of the air temperature by thermometers placed at the side of the box so that correlations with atmospheric temperatures could be made.

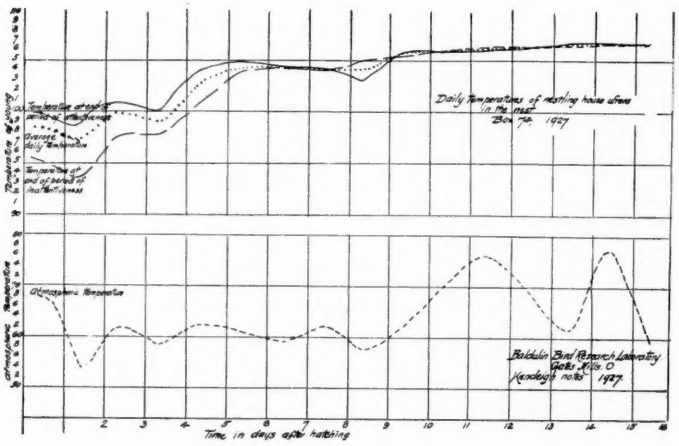
Daily Temperatures of nesting house wren in the west
Box No. 1927
Atmospheric Temperature
Baldwin Bird Research Laboratory
Oaks, Okla.
Kendeigh notes 1927
Time in days after hatching

FIG. 8

The average temperature of the young at the end of the periods of attentiveness and inattentiveness and from day to day are given in the table below and are further shown in the accompanying graph (Fig. 8). The average temperatures of the young at the ends of the periods were obtained by averaging all the readings. The average temperature of the young for each day was calculated by averaging the temperatures at the end of the attentive

TABLE 2

DAILY TEMPERATURES OF YOUNG HOUSE WRENS IN THE NEST

| Age in days | Temperature at end of period of attentiveness | Temperature at end of period of inattentiveness | Average temperature | Air temperature |
|---|---|---|---|---|
| —— (1st) | 99.8° F. | 95.4° F. | 98.6° F. | 68.0° F. |
| 1 (2nd) | 99.6 | 93.7 | 97.3 | 53.5 |
| 2 (3rd) | 100.8 | 97.6 | 99.9 | 61.5 |
| 3 (4th) | 100.0 | 97.7 | 99.0 | 58.5 |
| 4 (5th) | 103.8 | 100.7 | 102.6 | 62.5 |
| 5 (6th) | 104.8 | 103.8 | 104.2 | 61.0 |
| 6 (7th) | 104.3 | 104.2 | 104.2 | 59.0 |
| 7 (8th) | 104.3 | 104.0 | 104.2 | 62.0 |
| 8 (9th) | 103.0 | 104.9 | 104.2 | 57.5 |
| 9 (10th) | 105.8 | 105.3 | 105.6 | 62.0 |
| 10 (11th) | ..... | ..... | ..... | ..... |
| 11 (12th) | 105.9 | 106.3 | 106.2 | 76.0 |
| 12 (13th) | 106.2 | 106.3 | 106.3 | 69.5 |
| 13 (14th) | 106.7 | 106.6 | 106.6 | 61.5 |
| 14 (15th) | ..... | ..... | 106.7 | 77.0 |
| 15 (16th) | ..... | ..... | 106.7 | 60.0 |

and inattentive periods in proportion to the average lengths of these periods.

It will be noticed that the temperatures of the young varied consistently with those of the atmosphere during the first few days, but later in the period of nest life they were unaffected. The change of the body temperatures from a varying stage to a more or less stabilized one is as evident here as in the experiments under controlled conditions. As for the average temperature of the young

from day to day there is evident a very steady rise from 98.6° on the first day to 106.7° on the last. During the first four days this is somewhat fluctuating, but during most of the nestling period the rise in the body temperature from day to day is pretty consistent and approaches that of the adult. However, it is not until several weeks after the young leave the nest that their temperatures become indistinguishable from those of adults since they are liable to greater fluctuations.

The body temperature of all the nestling birds is not always the same at any one time. The position of any young bird in the nest in relation to his fellows is important. Ordinarily the young huddle or bunch together in the nest so that when the adult bird is away those on the outside of the huddle become cool faster than those in the middle because they are more exposed. Before the adults return, the birds on the outside may be two, three or more degrees cooler than those in the center. This discrepancy is greater during the first two or three days of nest life than later and it is greater also on cool days than on warm. However, when the female broods, those birds on the top of the pile are favored over those on the bottom or the sides so that when she leaves at the end of the attentive period they may be somewhat warmer or, more frequently, nearly the same.

One last method and set of data remain to be described. All the information thus far has been of birds during only a short period of the day, even though this period has amounted to several hours. It was thought desirable to get some data on the continuous temperature of the young, day and night, so that broader conclusions could be reached. This was done by means of the recording potentiometer connected to a thermocouple stretched across the bottom of the nest cavity. As the young were crowded in the nest and had to sit upon the bottom, they were in almost continuous contact with the thermocouple. A continuous record was thus obtained of the temperature of the ventral surface of the bird. This record is

most valuable before the young have developed feathers, but even afterwards a certain amount of information is obtainable.

In order to find out the relation between the surface temperature and the body temperature of the young birds simultaneous readings were taken by means of thermocouples and thermometers of the two temperatures. Several such determinations indicated that the belly temperatures obtained in the nest may be between two and three degrees lower than the actual body temperature of the bird and that as the bird becomes older and the feathers develop this difference may be greater. Nevertheless, our data justify the assumption that variations in the one are correlated with similar variations in the other, although possibly to a variable degree, and so the differences as such may be disregarded in interpreting the records obtained.

The difference in the amount of temperature variation in the young during daytime and night is quite marked. At night, when the adult female is constantly brooding, the temperature of the young is uniform. Occasionally there is discernible a slight lowering in the temperature from the first part of the night until early morning, but this never amounted to more than one or two degrees. During the day, on the other hand, the variation in young bird temperatures is extreme, particularly during the first few days out of the shell. During the first two or three hours in the morning, after the adults begin their morning activities, the temperature of the young is at its lowest point since the adults are brooding only a part of the time, and the air temperature is itself at or near its daily minimum. As the air temperature becomes warmer during the day the temperature of the young also rises so that during early afternoon it reaches the maximum. There is usually then a decline until night. Occasionally just before dark before the adult has gone into the box to brood for the night the temperature of the young again drops quite a little, although it is usually never quite as

much a drop as during early morning. The temperature of the young at night is lower than while being brooded during the day, but is generally higher than when the adult is not brooding. The temperature of the young is distinctly correlated with atmospheric temperature variations since the two closely follow each other, although that of the young birds is necessarily more fluctuating. When there is a distinct daily rhythm in the air temperature, there is also one in the temperature of the young birds, but when there is none or very little the temperature of the young is more uniform. The maximum points in the air and bird rhythms come at approximately the same time. It may be stated on the side that variations in the air temperature were obtained by means of a Tycos thermograph placed at one side of the nest box in a shelter.

Surface temperatures of the young were also taken with the use of the indicator potentiometer for brief periods to check up the results of the recording instruments. This brought out, among other things, that even in the nest when the young birds are active and moving around their temperatures may occasionally be lower than when they are quiet. This was what was found to be the case with the older young birds under controlled conditions, as has already been stated. However, the loss of heat is less when the birds are active in the nest, as when receiving food, since the birds are crowded together and the nest itself is lined with feathers, besides being in a box. This drop in temperature when moving around and possibly also when receiving cold masses of food may help to explain the instances (Fig. 8) when the temperature of the nestling birds at the end of the attentive feeding period was less than what it was at the end of the inattentive period.

## V. Discussion of Results

Very little needs to be said further in interpreting the results of the experiments above described. A few points

are, however, of such special interest as to warrant some extra attention.

Adult birds are ordinarily considered to be hot-blooded animals having a stable temperature which groups them with the mammals as homoiothermic. Birds should not, however, be thought of as having a certain degree of temperature which they maintain persistently; rather they should be considered as having a distinct range in temperature, which may amount to several degrees. That they have a variable temperature should not throw them out of the group of warm-blooded animals, since temperature of man himself is not absolutely uniform but varies one to two degrees day and night. The variable temperature in adults seems not directly correlated with atmospheric temperature.

With young birds the situation is different. Here the temperature is extremely variable and if the young bird was dependent upon its own resources for heat it would be as truly a poikilothermic or "cold-blooded" animal as are many invertebrates. Especially is this the case with the very young birds which have just broken out of the shell. This similarity is further enhanced by marked variations in behavior and activity at different degrees of temperature. During the life in the nest the bird develops, however, an efficient control system so that when it leaves the nest its body temperature is more nearly uniform. Thus if we consider the young bird as an isolated individual it develops from a cold-blooded animal into a warm-blooded one during the period in the nest. A similar development appears also to occur in the ontogeny of mammals and even man (Pembrey, 1895; Kimber and Gray, 1923).

That this fact is of significance in the phylogeny of the class is at once evident and suggests that the immediate pre-avian ancestors were cold-blooded. The same suggestion also holds for the class Mammalia. However, warm-bloodedness probably developed independently in the two classes since the method of temperature control in the two groups has many quite dissimilar points.

Actually, however, the variation in the young birds' temperature in the nest is not so great as it would be if the air temperature were the only factor involved. Due to the brooding of the adults the variation in its temperature is kept within a ten to fifteen degrees limit at the extreme. High metabolism and consequent high rate of development can only take place when the temperature is at its optimum, and so it is of distinct advantage to both the young and the adults that their body temperatures be maintained. That young house wrens are capable of surviving for long periods without the brooding of the adult is shown by one case where late in the season a single young bird just out of the shell was abandoned by the parents, yet survived for more than three days and nights alone in the nest, and possibly then died more from want of food than from chill. However, the bird did not increase in size or weight or show any other evidence of growth.

The development of temperature control in nestling wrens is correlated with the activities of the adults, since brooding is the main feature of their attentiveness during the first few days and almost absent, except at night, during the last few days.

No extensive comparative studies were made in this work on young birds of other species. There is, however, good reason for believing that the condition of nestling house wrens in regard to temperature regulation and development of a temperature control is duplicated throughout the class of altricial species. Pembrey (1895) states that the power of heat regulation is well developed in young pigeons by the fifteenth or sixteenth day. With species hatching their young in a precocial state of development, as in the domestic fowl, the situation is different. Pembrey, Gordan and Warren (1894–'95) state that "the developing chick during the greater part of the period of incubation responds to changes of external temperature in a similar manner to that of a cold-blooded animal; that towards the end of incubation,

about the twentieth or twenty-first day, there is an intermediate stage in which no marked response is observed, and this apparently neutral condition is succeeded, when the chick is hatched, by a stage in which the chick reacts as a warm-blooded animal." Thus it would appear that the young of precocial species are homoiothermic at birth and that the poikilothermic stage is passed through while still in the shell.

## VI. Conclusions

(1) The obtaining of bird temperatures with the use of thermocouples is more accurate and efficient than with the use of mercury thermometers of the types described, although for certain things both may be used to advantage.

(2) Under natural nest conditions, due to differences in atmospheric and brooding temperatures, the body temperatures of young house wrens vary several degrees during the first few days out of the shell, but by the time they are ready to leave the nest their temperatures are not only higher but distinctly less variable. Thus, in their development, the young birds pass from a poikilothermic state to a homoiothermic one.

(3) The development of a resistance in young house wrens against cold follows the sigmoid growth curve. This development of temperature resistance is due primarily to the mass of body increasing faster proportionately than the external dissipating surface, to the development of a feather covering, to the development of an internal dissipating surface probably under nervous respiratory control, and to the production of heat in the metabolism of the bird. Of these four factors, the third is apparently the most important.

(4) No efficient resistance against extreme heat is developed in young house wrens, although rapid respiration from the lungs and air sacs probably serves toward this end.

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# SHORTER ARTICLES AND DISCUSSION

## ECTOPARASITES AND VITALITY

THE relationships between parasites and their hosts have been rather intensively studied, but I believe that the experimental study of the effects of ectoparasites on the general vitality of their hosts has been somewhat neglected. The literature on the ectoparasites of fishes, though extensive, is chiefly concerned with the statics rather than the dynamics of the described relationships.

For the present purpose I shall simply understand vitality to be a function of the general viability or ability to survive. But the general viability must be the summation of the specific viabilities under specific external situations. It remains then to obtain indices of a number of representative specific viabilities in order to approximate to a quantitative expression of vitality. This may be done by measuring the time-survival of the organisms studied in various external situations in each of which there is a known unfavorable factor. A comparison of the effects of these various factors is of much interest.

In practice it would appear that in attempting to measure the effect of some factor (say isopod parasitism), on the general vitality (of fish in this case), we frequently encounter situations where our crude methods do not reveal any marked effect of the factor by itself. We are forced, then, to use several combinations of unfavorable factors and solve, by elimination, for the share in the result ascribable to the desired factor.

Work was begun in this laboratory some months ago on the general question of the selective action, in fish, of semi-lethal environments. The type fish used was the Pacific marine killifish, *Fundulus parvipinnis*. It was early noted that in each sample taken a rather constant small proportion of the individuals were parasitized by isopods (*Livoneca californica* Schioedte and Meinert), of such size that a single parasite often made its presence in the gill chamber known by causing a marked protuberance of the operculum. For example, an isopod measuring 11.4 mm. in length was removed from a fish of total body length 59.6 mm. Close check of the deaths under good aquarium conditions (running sea-water, good food, etc.), failed to reveal any harmful effect of the parasites. Even partial

starvation apparently did not affect the equality of the death-rates of normal and parasitized fishes.

It at once occurred to me that the harmful effect of the presence of the parasites might be fairly definitely measured by its influence on the death-rate of the fishes when subjected to various semi-lethal environments. Fresh collection samples were taken and the relative viabilities of the individual fishes under experimental conditions of low oxygen tension (and concomitant high $CO_2$ tension) and suddenly lowered salinity were determined, using the time-survival as an index. The lower resistance of the parasitized fishes was clearly shown under both experimental conditions. A total of 565 fishes were used, 281 being subjected to progressive asphyxiation conditions in three experiments, and 284 in four experiments involving sudden decrease of salinity and osmotic pressure. Of this number thirty-seven fishes, or 6.5 per cent., each contained from one to three isopods in the gill chambers. The death-distribution of these parasitized individuals is shown in the table where they are entered according to the relative time at which they succumbed.

DECILS OF TIME-SURVIVAL[1]

| | No. of fishes | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Total | Average decil |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Asphyxiation | 281 | 8 | 3 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 14 | 2.22 |
| Low salinity | 284 | 14 | 6 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 1.52 |
| Totals | 565 | 22 | 9 | 3 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 37 | 1.78 |

It is striking that the relative resistance of the parasitized fishes was so low that more than four fifths of them died before one fifth of the total number of fishes had succumbed. Furthermore, at least with the particular technique used, it is suggested that the deleterious effect of the parasites is more marked in decreased salinity than in low oxygen tension. However, it is not claimed that this difference is entirely a question of oxygen and salinity; there were, of necessity, other differences between the two series of experiments (*e.g.*, temperature, and the time factor), which, though slight, might possibly account for the difference.

[1] Decil No. 1 represents the first 10 per cent. of the fishes in the experiment to die, etc.

The question as to the permanence of the effects produced by a limited period of attachment of the isopod to the host has not been given special treatment here as yet, but there is good evidence to show that there is no serious injury involved. At the close of an asphyxiation experiment not included above some thirty fishes were removed as dead. They were placed in a ten liter glass jar of water agitated by a strong stream of oxygenated water and closely observed. At the end of two hours, fourteen showed some signs of life; the dead were removed and the living, still unable to swim, were examined. Two fishes contained isopods in the gill chambers; the parasites were removed, the entire fourteen fishes were segregated in separate jars of oxygenated water and kept under observation. The revived fishes began to die in twelve hours, but the two individuals which had been parasitized outlived all the other twelve by a good margin (24 and 188 hours, respectively).

The influence of these ectoparasites on the rate of growth and differentiation is an important point which deserves more investigation. It is interesting that the parasitized fishes consistently averaged slightly smaller in body length than the sample in which they were taken; this difference was, however, well within the range of the normal individuals. The average of all fish was 56.6 mm; the average of the parasitized fishes was 51.4 mm.

As far as I am able to ascertain, the experimental demonstration with fishes of the relationships indicated above is not to be found in the literature. I am informed separately by Dr. Edwin Linton, whose extensive work on fish parasites is well known, and by Dr. Maurice C. Hall, chief of the Zoological Division of the Bureau of Animal Industry, U. S. Department of Agriculture, that they are unaware of such work. A recent communication from Professor Charles B. Wilson, well known for his studies of the parasitic copepods, is of much interest. I quote in part:

> . . . After many years of study of the ectoparasites of fishes I have come to the conclusion that as long as the fish remain healthy in other respects and are not subjected to adverse conditions a reasonable number of parasites do not apparently produce harmful effects.
>
> I am willing to go farther and say that I have repeatedly seen fish so loaded with these external parasites that it seemed to me a wonder they did not die. And yet as far as could be determined they were as lively and healthy as long in an aquarium as others that were free from parasites.

On the other hand . . . I fully believe in your idea of a relationship between parasitism and adverse conditions. To the best of my knowledge it has never been demonstrated experimentally. . . . It is a phase of the general problem of fish ecology which has apparently escaped attention thus far but which may well have far-reaching influence.

The evidence presented here is conclusive on certain points and is suggestive on others. We are justified in assuming, as a basis for further work, that ectoparasites may exert a deleterious influence on the general vitality which becomes extremely important under adverse conditions. By the method outlined above it is possible to determine the general order of magnitude of that influence. It is probable that ectoparasitism is associated in some way with the gross size of the host, either as a cause or an effect of impairment of the growth processes. Finally, the harmful effect of the presence of the parasites may vary as to magnitude in the presence of different second adverse factors.

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## A PRELIMINARY NOTE ON THE OCCURRENCE OF HAPLOIDS IN CREPIS

IN the family *Solanaceae* plants with the haploid chromosome number are not very rare occurrences, over fifty having been reported in *Datura stramonium*,[1] eight in *Solanum nigrum*[2] and seven in *Nicotiana tabacum*.[3] Among other flowering plants, however, the only cases of haploid sporophytes recorded have been that of one plant of *Triticum vulgare*[4] and that of one "disomic haploid" in *Matthiola incana*.[5] The chromosome numbers of these species are as follows: *Datura stramonium*

[1] Blakeslee, A. F., Morrison, G., and Avery, A. G. Mutations in a haploid *Datura* and their bearing on the hybrid-origin theory of mutants. *Jour. Hered.*, 18: 193–199. 1927.

[2] Jörgensen, C. A. The experimental formation of heteroploid plants in the genus *Solanum*. *Jour. Gen.*, 19: 133–211. 1928.

[3] Ruttle, Mabel L. Chromosome number and morphology in *Nicotiana* species II. Diploidy and partial diploidy in root tips of *tabacum* haploids. Univ. of Cal. Pub. in Bot., 11. In press.

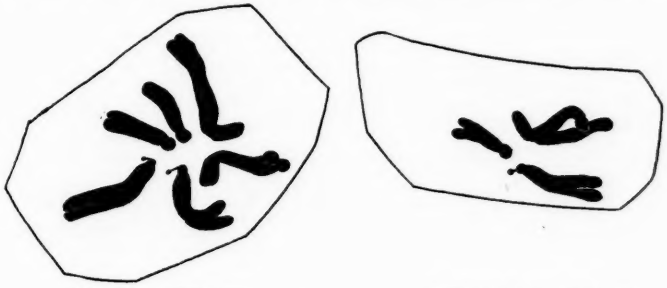
[4] Gaines, E. F., and Aase, Hannah C. A haploid wheat plant. *Amer. Jour. Bot.*, 13: 373–385. 1926.

[5] Lesley, Margaret M., and Frost, H. B. Two extreme "small" Matthiola plants: A haploid with one and a diploid with two additional chromosome fragments. AMER. NAT., 62: 22–33. 1928.

n = 12, *Solanum nigrum* n = 36, *Nicotiana tabacum* n = 24, *Triticum vulgare* n = 21 and *Matthiola incana* n = 7. To this list may now be added two haploid plants of *Crepis capillaris,* a species of the *Compositae* which has the smallest known chromosome number (n = 3) in flowering plants.

Like most of the haploids recorded these occurred in $F_1$ progenies of a species cross. Nearly 1,700 $F_1$ hybrids of *Crepis capillaris* and *C. tectorum* are being grown this spring and among these two plants which have proved to be haploid *C. capillaris* have been found. They arose in populations of hybrids in which different plants of *C. capillaris* were the female parents and from crosses made on the same day. The parental plants were kept in an unheated greenhouse. Examination of weather records showed that the temperatures prevailing at that time were low and that the minimum for the night following the making of these crosses was the lowest recorded during the four months when hybridizing was being carried on. Some of the *Datura* haploids were progeny of plants treated with cold, but most of the haploids recorded have been regarded as the result of the development of unfertilized egg cells stimulated by the growth of foreign pollen on the stigma. Whether it was low temperature or the *tectorum* pollen or both which were contributing factors in this case is of course unknown.

Still in the rosette stage, the plants are much smaller than normal *C. capillaris* but healthy. They resemble the diploid, but the leaves are shorter, narrower and less deeply indented. They were sufficiently different from $F_1$ hybrids and from the female parent to merit cytological study and their haploid con-



Diploid *C. capillaris* Haploid *C. capillaris*

FIG. 1. Somatic metaphase plates from root tips of diploid and haploid *Crepis capillaris.*

dition was thus established. The material available for examination up to the present has been limited to a few root tips from each plant. The cell size is smaller in the haploids and the figure which shows the diploid and haploid chromosome complexes seems to indicate that the chromosomes of the haploid may be somewhat reduced in size. That one chromosome of each pair is present is, however, quite clear. The three chromosomes may be clearly recognized in late prophases and in anaphases as well as in the metaphases of dividing cells.

In roots of one of the two plants diploid tissue has been found. Of three roots examined one showed only diploid plates, and each of the others had a small diploid area, in one case in the central cylinder, in the other in the outer cortex. Presumably the diploidy has resulted from doubling of the haploid complex. A similar phenomenon has been found in haploid *Nicotiana tabacum* by M. L. Ruttle. It is hoped that further study will reveal the extent and mode of origin of the diploid tissue. It is possible that it will increase in amount with the age of the plant and that portions above ground may become diploid. The hope of securing normal gametes and viable seeds is therefore increased.

The occurrence of these haploids has raised hopes of securing them in other species and of obtaining homozygous races which will be of value in genetic studies. If they mature the small number of chromosomes should make them favorable material for a further study of meiotic phenomena in haploids.

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## THE CHROMOSOME CONSTITUTION OF THE LITTLE AND BAGG ABNORMAL EYED MICE[1]

IN 1924 Little and Bagg reported the occurrence of four heritable morphological variations in the progeny of mice which had been exposed to X-rays. Among these characters was an eye defect which was non-lethal, behaved as a mendelian recessive in crosses, and since it appeared only in the X-rayed

[1] Contribution No. 213 from the Department of Zoology, University of Texas. Professor H. J. Muller called my attention to the desirability of studying these mice.

stock may have been produced by this agency. Granting this assumption, it does not necessarily follow that a true mutation had been produced, that is, that changes were induced in one or several closely linked genes, for it is possible that the defect is conditioned by an induced anomalous chromosome constitution resulting in a "genic unbalance" which takes this expression. The facts which suggest the latter possibility are discussed below.

Cytological studies of X-rayed animal tissue have clearly shown that this agency affects the chromatin of the cell, the character of the injury varying with the length and intensity of exposure and the phase of mitosis in which the cell happens to be when exposed. In general, there is a "primary effect" usually expressed by a breaking up (transverse fragmentation) of the chromosomes (exposed during mitosis), then there is a latent period when active mitosis is suppressed followed sooner or later by renewed mitotic activity when the "secondary effect" is observed.[2] This last seems to cause the two halves of a dividing chromosome to stick together especially at the ends. Both the primary and secondary effects of irradiation would seem to offer an excellent opportunity for an abnormal distribution of chromatin. When germ cells are exposed, as in the case with which we are dealing, we might reasonably expect to find some of the progeny with abnormal chromosome constitutions.

That abnormal characters may appear as a result of genic unbalance when the normal chromosome constitution is disturbed is well known. Either the presence of an extra chromosome or the absence of one or even of a part of one has a marked effect. (For example, the 2n+I Daturas or Oenotheras, the haplo- IV individuals of D. melanogaster, Gates non-disjunction mice). In view of the exceptional interest which centers about the production of mutations through external agencies, it seemed desirable to examine the chromosomes of abnormal-eyed mice to determine if this defect might be conditioned by an abnormal chromosome constitution.

Dr. C. C. Little very generously sent me four abnormal eyed male mice for cytological study. These were castrated and the testes preserved and treated as in my other mammalian chromosome studies.

[2] For review of the literature on this subject see Alberti and Politzer, 1924. *Arch. f. Mikr. Anat.*, vol. 100.

An examination of the chromosomes of all four males failed to reveal any abnormal chromosome conditions. The spermatogonial chromosome number is 40 in each case (the normal diploid number), and a careful examination of the individual elements both in spermatogonia and in primary spermatocytes has disclosed no abnormal features. A large number of counts were made for each male and many primary spermatocyte spindles were carefully analyzed during the course of this study. Frequent comparison was made also with normal mouse chromosomes and with the chromosomes of Gates' non-disjunction mice which exhibit a chromomere deletion. As far as the writer has been able to determine, the chromosomes of the abnormal eyed mice are normal in number and morphology.

It may be concluded, therefore, that as far as the cytology of these mice is concerned there is no evidence that the defective eye is conditioned by chromosome abnormalities.

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## THE VARIATION OF *LYMNÆA TRASKII* TRYON IN POND AND LAKE HABITATS

IN the course of a study of the molluscan fauna[1] of Jasper National Park, Alberta, Canada, during the summers of 1925 and 1926, a great deal of variation was noticed in the shells of a number of species. In order to gain a better understanding of the nature of this variation, several series of shells, representing some of the most abundant species, have been carefully measured. The most definite results have been obtained in the case of *Lymnæa traskii* Tryon. In this case two series were measured, one from the shores of a large lake, and the other from a small pond. As the differences between the two series are quite clear cut it has been thought that they would be of sufficient interest to merit publication.

One series of shells was collected on an exposed stony shore of Maligne Lake, Alberta, which is the largest glacier-fed lake in the Canadian Rockies. The other series came from a small

[1] An account of the systematics and local distribution of these forms has been prepared and will be published shortly in the "Contributions to Canadian Biology."

pond, near the Upper Maligne River, a stream which empties into Maligne Lake about two miles west of the foot of Mount Charleton. The water in this pond was only two feet in depth. The diurnal range of temperature was undoubtedly far greater in this pond than in the lake, as the nights in this northern region are bitterly cold even in midsummer. Severe frosts occurred frequently during our stay. Both habitats are at the same altitude, 5,500 feet above sea level. The shells have been carefully examined and there is no doubt as to their being *Lymnæa traskii*. The individuals of both series belong to a rather ovate form of this species.

It will be seen in the accompanying table that the dimensions of the shells from the pond are in all cases greater than those of the specimens from the lake. This information is not conclusive as there is no means of determining the relative ages of the shells of the two series. The standard deviations in these cases serve only to indicate the relative homogeneity of the two series. However, when the ratios of the various dimensions of the shells to one another are compared it is readily seen that the shells from the pond are considerably longer, relative to the width of the shell (greater diameter) and to the length of the aperture than are the lake shells. The size of the aperture is also greater, in the pond individuals, and the width of the shell relative to the width of the aperture is also greater. The mean values for these ratios in the pond shells approximates, and in two cases exceeds those of the lake shells. It is interesting to note that with respect to two groups of organisms of the same species type, living in adjacent but different types of habitat, the differences in the dimensions of the shell in groups of individuals taken at random may be shown to be not only marked but consistently so, ranging as indicated by the values for range differences in the table in all the ratios from 27½ per cent. to 60½ per cent. greater. In other words, the snails from the pond are more variable as regards the shell characters given than are the lacustrine individuals. The explanation of this lies perhaps in the presence of a greater food supply and higher maximum temperature in the pond than in the waters of the glacier-fed lake. The ratios were selected on the basis of a supposed possible relationship in the morphological growth relation of the organism. While these cannot be applied consistently without a progressive series of measurements made during the various stages

COMPARISON OF THE SHELLS OF *Lymnæa traskii* TRYON FROM POND AND LAKE HABITATS

| | Maligne Lake | | | | | Pond near Upper Maligne River | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | A. M. | S. D. | H. V. | L. V. | Range or Limit | A. M. | S. D. | H. V. | L. V. | Range or Limit |
| Length | 10.0 | .74 | 12.4 | 8.6 | | 12.7 | 1.4 | 16.1 | 10.5 | |
| Greater Diameter | 5.5 | .49 | 6.9 | 4.9 | | 6.6 | .87 | 8.0 | 5.2 | |
| Lesser Diameter | 4.8 | .42 | 5.8 | 4.2 | | 5.8 | .71 | 6.9 | 4.8 | |
| Aperture Length | 5.5 | .46 | 6.7 | 4.6 | | 6.7 | .92 | 8.5 | 5.1 | |
| Aperture Width | 3.5 | .35 | 4.3 | 3.2 | | 3.8 | .62 | 5.0 | 3.0 | |
| $\frac{\text{Length}}{\text{Greater Diameter}}$ | 1.80 | .70 | 1.94 | 1.65 | .29 | 1.92 | .94 | 2.19 | 1.79 | .40 |
| $\frac{\text{Length}}{\text{Aperture Length}}$ | 1.79 | .64 | 1.90 | 1.66 | .24 | 1.88 | 1.3 | 2.23 | 1.73 | .50 |
| $\frac{\text{Aperture Length}}{\text{Aperture Width}}$ | 1.55 | .68 | 1.68 | 1.43 | .25 | 1.75 | 1.01 | 2.00 | 1.60 | .40 |
| $\frac{\text{Greater Diameter}}{\text{Aperture Width}}$ | 1.55 | .46 | 1.65 | 1.43 | .22 | 1.71 | .88 | 1.97 | 1.56 | .41 |

Dimensions of shells and the corresponding standards derivations are given in millimeters.

Explanation of Abbreviations.

A. M.—Arithmetic Mean.
S. D.—Standard Deviation or Error of the Mean Square.
H. V.—Highest Value.
L. V.—Lowest Value.

in the growth of the organism, they may be assumed for practical purposes to be in some degree interdependent.

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